

18.

STUDIES OF EOCENE MAMMALIA IN
THE MARSH COLLECTION,
PEABODY MUSEUM.
PART II. PRIMATES.

WITH TWO PLATES.

By J. L. WORTMAN.

(Uncompleted.)

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOLS. XV-XVII, 1903-1904.]



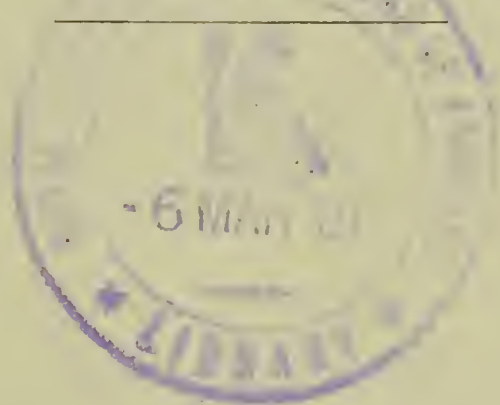
NOTE.

As stated in the introduction to Part I. of these studies, it was the intention of Dr. Wortman to give a "study of the more important materials in the splendid collection of Eocene Mammalia in the Marsh Collection of the Peabody Museum, with the object of presenting a full account of the structure and relationship of those forms, as far as revealed by the remains at present known." Conditions have since arisen in consequence of which the author has decided to terminate at this point his work on this collection.

CHARLES SCHUCHERT,
Curator Department of Geology.

YALE UNIVERSITY MUSEUM,
October, 1905.

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XV, MARCH, 1903.]



PART II. PRIMATES.

INTRODUCTION.

SOMEWHAT contrary to the accepted order of arrangement usually adopted in treating of the Mammalia, I select next for consideration the Primates, a perfectly natural and homogeneous order, including the Lemurs, Monkeys, and Apes, as well as Man himself. This latter fact invests the study with more than ordinary importance, inasmuch as any additional evidence bearing upon the past history of the group to which man belongs cannot fail to prove of the highest interest, even though it throw only a side light upon the development of the human kind. In view of the belief that the general current of opinion seems to be setting strongly in the direction of the conclusion that the ancestry of the human species, with all its endowments, both mental and physical, must be sooner or later traced with certainty to this source of origin, we may be pardoned for a somewhat exhaustive presentation of the facts which our fossils exhibit.

The various groups of Mammalia have been developed and specialized along diverse lines, the primary cause of which we may regard as having been due to adjustment to varying conditions of environment. It thus happens that different sets of organs have been involved in these changes, so that when we attempt the classification and definition of a natural group, we seek to learn what structures have been most profoundly affected. In the case of the Primates, the enlargement and specialization of the cerebral lobes of the brain constitute the

character *par excellence* in which they have made the greatest progress and in which their evolution has been most marked. The very early development of prehensile hands and feet and the better arrangement of the cerebral circulation have been intimately associated with this progress and are therefore factors of prime taxonomic value and importance. In other words, the Primates have adapted themselves more widely to environment than any other mammalian group, in consequence of which they present well-defined skeletal indices or equivalents, so that whenever they are sufficiently preserved, it is possible to recognize them with a degree of certainty not usually found in other groups of the Mammalia.

Characters of the Cerebral Circulation.

As regards the first set of these characters (the enlargement of the brain), like all other specialized features which come to distinguish a group or order in the final or advanced stages of its evolution, they are of necessity less distinctly marked in the earlier representatives than in the later ones; so that, as we approach the point of origin, greater and greater difficulties are experienced in the application of such characters as a real test of affinity. Thus it is that we find in the less specialized members of the Primates, such as the lemurs and the oldest true monkeys, the relative development of the cerebral hemispheres to be little, if any, greater than that of many of the Insectivora; and were we compelled to depend upon this character alone, it would be in many instances practically impossible to determine whether the animal in question were a Primate or an Insectivore.

Fully recognizing the importance of thus clearly distinguishing between these small-brained Primates and other contiguous groups, in the matter of certain cranial characters, I have been led to make a careful and somewhat exhaustive study of the manner in which the blood supply is furnished to the cerebral hemispheres. Especial attention to this subject has been given, on the assumption that it must have been not only intimately associated with the progressive enlargement of the cerebral hemispheres in the Primates, but was in a way not now clearly understood, in some degree at least, responsible for it. If it is true that certain fundamental differences of this character exist between the several orders, the practical advantage to the paleontologist will be great, since it is only on very rare occasions that he has to deal with complete skeletons of the extinct species. In order to bring out these characters more clearly, I shall first consider the Insectivora, and I begin by quoting Huxley's statement of the course of the entocarotid in the hedge-

hog, figure 100. He says :* “The course of the internal carotid artery is remarkable. When it reaches the base of the skull it enters the tympanum and there divides into two branches, of which one traverses the stapes, and, passing forward in a groove of the roof of the tympanum, enters the skull and gives rise to the middle meningeal and ophthalmic

100

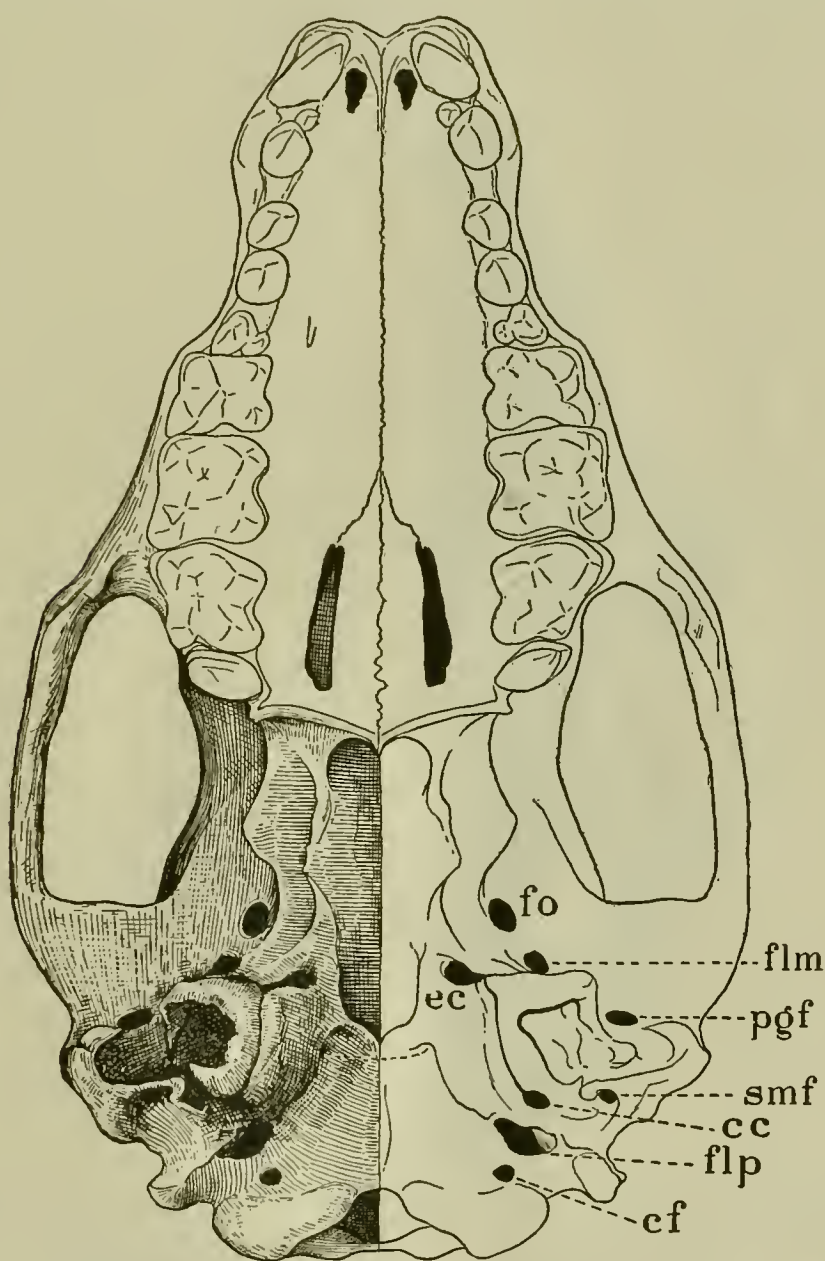


FIGURE 100.—Enlarged view of the base of the skull of *Erinaceus europæus*; showing the foramina.

fo, foramen ovale; *flm*, foramen lacerum medium; *ec*, eustachian canal; *pgf*, postglenoid foramen; *smf*, stylomastoid foramen; *cc*, carotid canal; *flp*, foramen lacerum posticum; *cf*, condyloid foramen.

arteries. The other branch passes over the cochlea, enters the skull by a narrow canal near the *sella turcica*, and unites with the circle of Willis.”

This course and distribution of the entocarotid is not only characteristic of the hedgehog, but is also found in the follow-

* Anatomy of Vertebrated Animals, 1872, p. 380.

ing additional genera of the Insectivora: viz., *Gymnura*, *Tupaia*, *Talpa*, *Scalops*, *Condylura*, *Sorex*, *Myogale*, *Centetes*, *Hemicentetes*, *Ericulus*, *Solenodon*, *Chrysochloris*, *Leptictis*, and *Ictops*. This list, it will be seen, includes typical representatives of all living families except the Macroscelidæ and Potamogalidæ. I have not been able to examine the skulls of any members of these two families, but I have very little doubt that it is true of them also, and that this course of

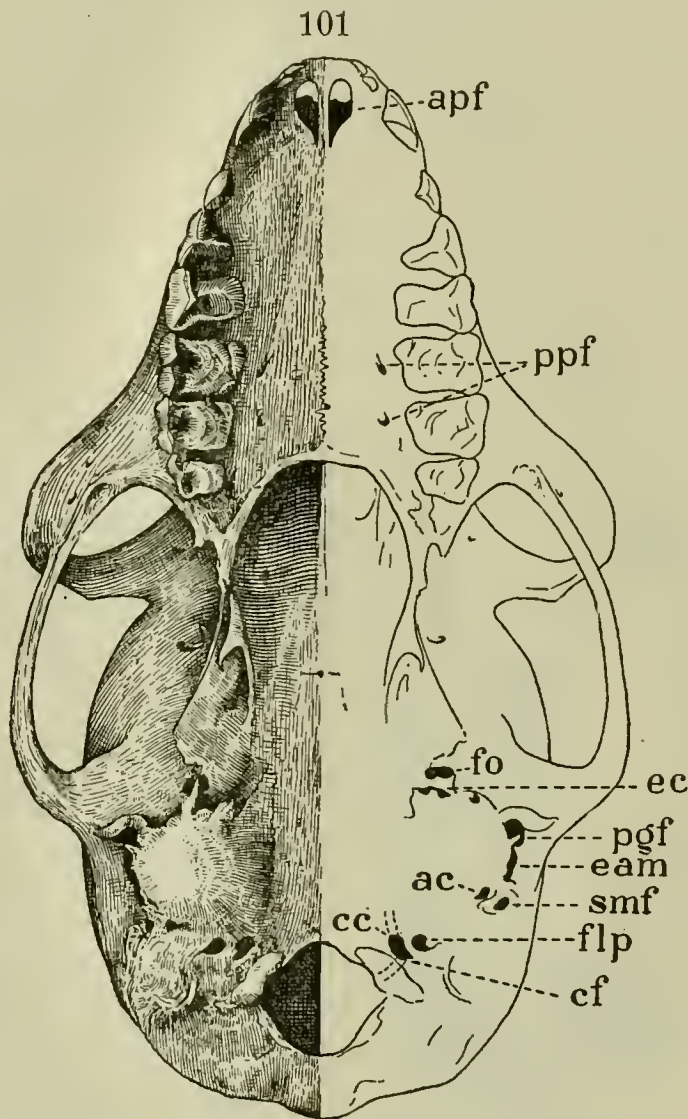


FIGURE 101.—View of the base of the skull of *Lemur catta*.

apf, anterior palatine foramen; *ppf*, posterior palatine foramina; *fo*, foramen ovale; *ec*, eustachian canal; *pgf*, postglenoid foramen; *eam*, external auditory meatus; *ac*, accessory carotid canal; *smf*, stylomastoid foramen; *flp*, foramen lacerum posticum; *cc*, carotid canal; *cf*, condyloid foramen.

the artery is a constant and important diagnostic feature of the Insectivore skull. It is of interest to note that in *Galeopithecus* the course of the artery is not like that in other Insectivora, but agrees with that of the bats and one important group of the lemurs. It may be also added that this course of the artery, according to Owen,* is true of some, if not all, Rodentia. The practical application of this knowledge of the course of the entocarotid, to the classification of certain fossil

* *Anatomy of Vertebrates*, 1868, vol. iii, p. 229.

forms of supposed Insectivora, is thus rendered possible by the distinct grooves which both branches make in the under side of the petrosal. In the case of all the recent forms which I have examined, as well as of some of the well-known fossil types, the direction of the two branches can be determined with ease.

Turning next to Primates, we find that in certain of the lemurs, notably the Indrisinæ and Lemurinae, the main branch of the entocarotid artery enters the cranial cavity through a canal at the postero-internal junction of the tympanic bulla and the basioccipital, near the point of exit of the condyloid foramen, figure 101. The main artery passes forward and into the cranial chamber at the side of the *medulla*, wholly within the posterior or cerebellar fossa. In some species of these two sub-families, there is a small canal entering the bulla in the position corresponding to the foramen for the entocarotid in the Insectivora; this is undoubtedly the homologue of the entocarotid in that group, but it is small and inconsiderable, and appears to be practically absent in all except *Lemur* and *Propithecus*. In these two genera, especially the latter, the tympanic branch is nearly as large as the main artery.

In the remaining species of the living Lemuroidea, there is no canal for the entocarotid in the position above described for *Lemur* and *Propithecus*, but there is a large and conspicuous *foramen lacerum medium*, which has its usual position at the antero-internal angle of the petro-tympanic, figure 102. Mivart constantly spoke of this foramen as the carotid canal, and from certain distinctive evidences of an arterial vessel entering the cranial cavity in this situation, in many imperfectly prepared skulls of these species which I have examined, there can be apparently no doubt that the office of this foramen is the transmission of the main entocarotid artery. It will be thus seen that there are two distinct types of entocarotid circulation in the Lemuroidea, both of which are sufficiently distinct from the Insectivora to afford reliable diagnostic characters.

In the remaining Primates or Anthropeoidea, including *Tarsius*, the entocarotid circulation presents another arrangement. In this group, the course of the artery corresponds more nearly with that of the Insectivora, in that its canal traverses the petro-tympanic chamber. There is an important difference in the two, however, for in the Anthropeoidea the stapelial branch of the artery is wholly wanting. The canal pierces the bulla in its posterior moiety, and passing forward over the cochlea, enters the cranial chamber in the middle or cerebral fossa, near the posterior clinoid process, just in advance of the tentorial ridge. This is evidently a superior

arrangement to that seen in *Lemur* and *Propithecus*, for the reason that the blood is delivered more directly to that part of the brain which it is intended to supply.

The following variations in the position of the external opening of the canal may be noted: In *Tarsius*, figure 103, it is placed a little anterior to the external auditory meatus and

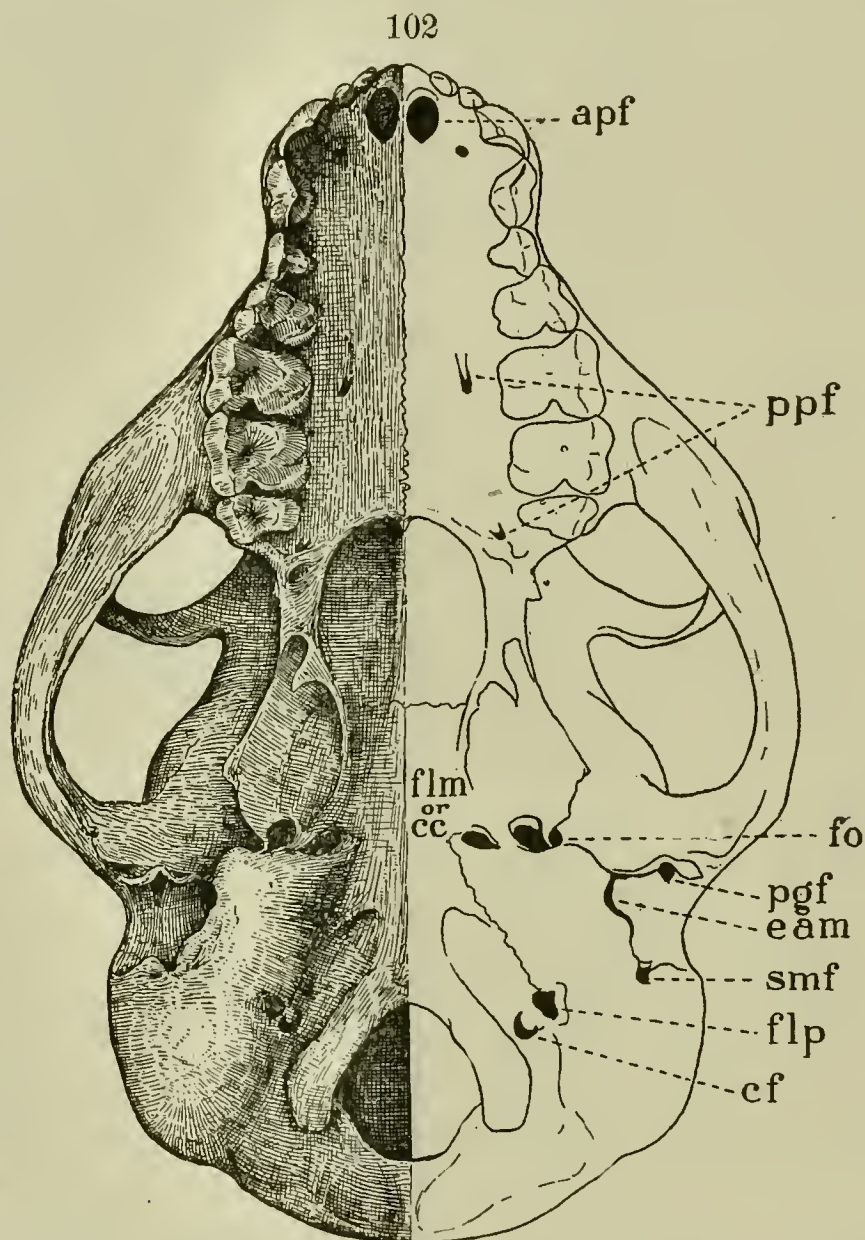


FIGURE 102.—View of the base of the skull of *Galago Montei*.

apf, anterior palatine foramen; *ppf*, posterior palatine foramina; *fo*, foramen ovale; *flm* or *cc*, foramen lacerum medium or carotid canal; *pgf*, post-glenoid foramen; *eam*, external auditory meatus; *smf*, stylomastoid foramen; *flp*, foramen lacerum posticum; *cf*, condyloid foramen.

rather to the outer than to the inner side of the bulla; in *Hapale* it is opposite the middle of the external auditory meatus upon the inner side of the bulla; in the Cebidæ, figure 104, it is yet more internal and somewhat more posterior;* and

* In *Hapale* and *Nyctipithecus* an interesting variation occurs. The main artery pierces the bulla in its usual position, but it apparently gives off a considerable branch, which enters the cranial chamber through a canal between the bulla and the basioccipital. This results in an arrangement similar to that found in *Lemur* and *Propithecus*, except that the position of the main branch is reversed.

in the Old World monkeys and the Anthropoids it has practically the same position as in the human species. In the extinct Eocene apes, as far as known, the main canal pierces the bulla in its posterior external portions. It should be here noted, also, that the relative size of the canal steadily increases from the small-brained to the large-brained forms, and that

103

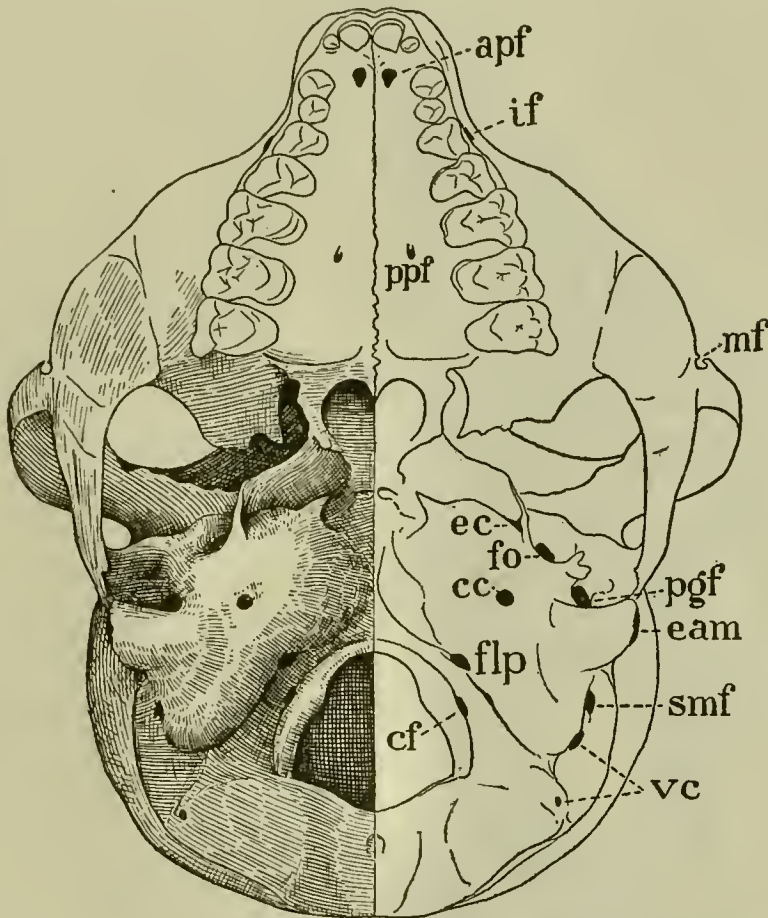


FIGURE 103.—Basal view of the skull of *Tarsius spectrum*; enlarged.

apf, anterior palatine foramen; *if*, infraorbital foramen; *ppf*, posterior palatine foramen; *mf*, malar foramen; *ec*, eustachian canal; *fo*, foramen ovale; *cc*, carotid canal; *pgf*, postglenoid foramen; *eam*, external auditory meatus; *smf*, stylomastoid foramen; *vc*, venous canals; *flp*, foramen lacerum posticum; *cf*, condyloid foramen.

this increase is directly proportioned to the degree of development of the cerebral hemispheres.

There yet remain to be described other characters of the blood supply to the brain through the vertebral arteries, in certain groups of the Primates, which are of importance from the standpoint of classification. In the lemurs,* the New World, and a few of the Old World monkeys, the course of the artery through the transverse process of the atlas is somewhat different from that seen in *Tarsius*, the anthropoid apes, and man. If the atlas of an anthropoid ape or man is viewed from behind, the large vertebrarterial canal will be

*The only exception which I have been able to find in this group is *Perodicticus potto*, in which the anterior bony bridge is not quite complete.

seen perforating the transverse process at its junction with the lateral mass of the bone. The anterior continuation of this canal is a deep groove turning sharply upward to reach a second perforation or deep notch in the anterior edge of the superior arch, at the upper extremity of the oval cup-shaped cotylus. This latter notch or foramen is known as the *sinus atlantis*, and serves for the entrance of the vertebral artery

104

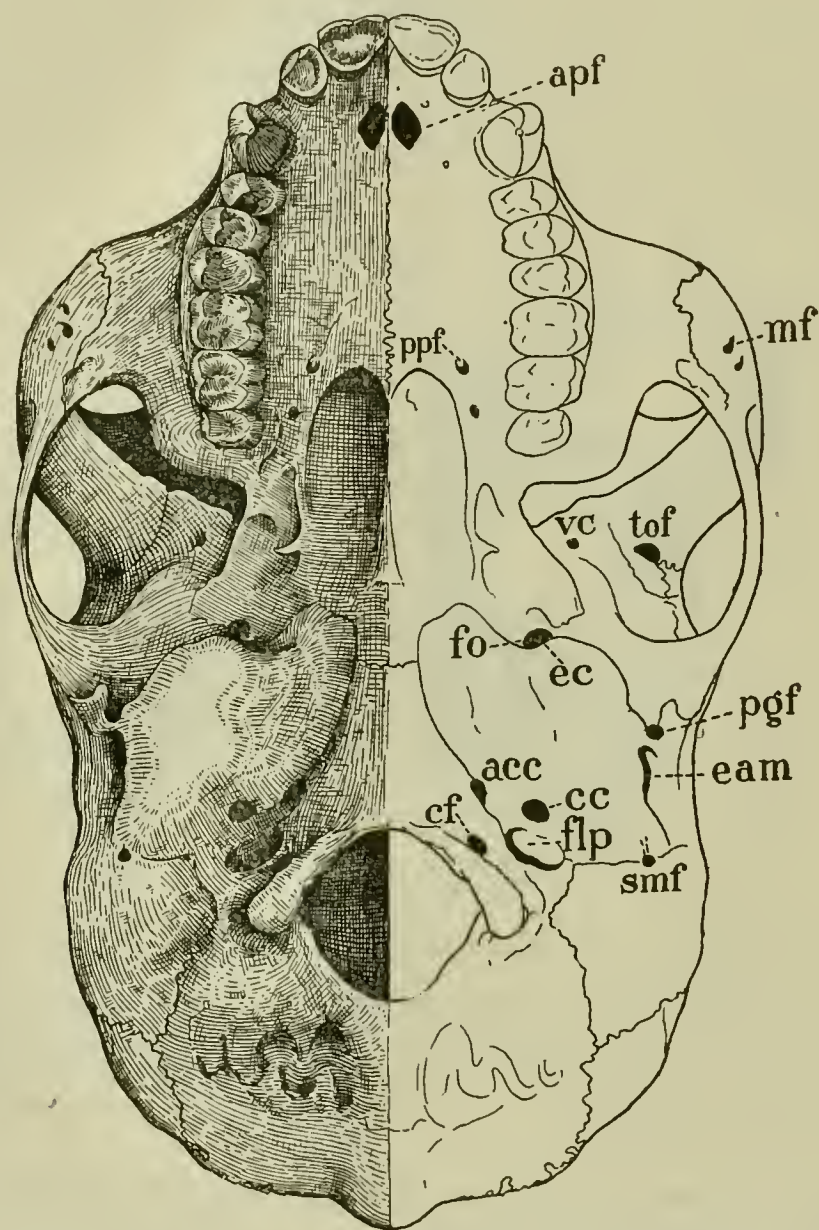


FIGURE 104.—Basal view of the skull of *Nyctipithecus felinus*.

apf, anterior palatine foramen; *ppf*, posterior palatine foramen; *mf*, malar foramen; *vc*, venous canal; *tof*, temporo-orbital foramen; *fo*, foramen ovale; *ec*, eustachian canal; *pgf*, postglenoid foramen; *eam*, external auditory meatus; *acc*, accessory carotid canal; *cc*, carotid canal; *smf*, stylo-mastoid foramen; *flp*, foramen lacerum posticum; *cf*, condyloid foramen.

and the exit of the first spinal or suboccipital nerve. Now, in the lemurs and lower monkeys, a strong bony bridge is thrown forward from the transverse process to the upper extremity of the cotylus, so as to cover in that part of the canal or groove where it turns sharply upward, and give separate openings for the superior and inferior (anterior and posterior of anthro-

potomy) divisions of the suboccipital nerve. This difference in the arrangement of the canal is constant and well marked, and serves as a reliable guide for distinguishing certain of the groups. The latter condition is also found in the Insectivora, and may be therefore looked upon as the more primitive of the two.

Finally, I may mention the absence of a separate opening (*foramen spinosum*), for the entrance of the middle meningeal artery into the cranial cavity, in all Primates except man.

Characters of the Prehensile Extremities.

The second set or group of characters of fundamental importance, by means of which the Primates are distinguished from all other orders of the Mammalia, relates to the modification of the hands and feet into more or less perfect prehensile or grasping organs, and in this respect they stand sharply apart from all other divisions of Eutherian mammals. Of the causes which led to this modification, very little is known, but there can be hardly any doubt that it was one of the primary distinguishing features of their remote Metatherian ancestors far back in the Mesozoic, and that its appearance constituted one of the first steps which led to their subsequent differentiation into such a distinct group. The particular type of extremity from which the prehensile modification arose was undoubtedly that of the plain plantigrade condition; and the assumption of an arboreal manner of life, we may readily believe, was the all-important determining factor in its evolution.

Exclusive of man, the Primates are, without exception, the most preëminently arboreal in habit of all the Mammalia. The arrangement of the thumb and great toe in opposition to the other digits, thus making it possible to take a firm hold or grasp upon the branches of a tree, is one of vast superiority to that in which the digits depend for their effectiveness upon sharp claws.

In the latter case, the claws serve as so many hooks by means of which the weight of the body is sustained in the act of climbing, whereas in the prehensile hand or foot of the Primates the hold is rendered effective by the opposability of certain of the digits to each other. The advantage of the grasping extremity over that which is solely dependent upon the hooked claws is seen in the ability of the animal possessing the former to traverse the forest without descending to the ground. Where the large branches of the adjoining trees interlace, the clawed animal experiences little difficulty in passing from one to the other, but if the trees are scattering, so that only the small branches touch, his progress is barred. To the animal with prehensile extremities, however, the case

is different; he simply runs out until he can gather a handful of smaller branches of the opposite tree, and swings himself across the interval with ease. Indeed, the skill displayed by monkeys in climbing surpasses that of any other animal.

It is of course not now possible to discover just what combination of circumstances first led the ancestors of the Primates to adopt an arboreal habit; it may have been for the purpose of greater protection from enemies, it may be that certain kinds of food, such as fruit and nuts, attracted them to the trees, or it may have been both; but, whatever the cause, it appears certain that this manner of life was adopted very early in their career, and has been responsible for one of the most important structural modifications which they now exhibit.

Another matter of great interest in connection with the prehensile extremities relates to their probable influence upon the growth of the cerebral hemispheres, as well as the general increase in intelligence in the Primates. No very complete phyletic history can as yet be made out for any existing species of monkeys, but such evidence as is obtainable demonstrates very clearly that the brain has increased in size over and above that found in the earliest forms. In some instances, this increase has been less marked than in others, but there has been, nevertheless, a gradual development of the cerebral hemispheres in all groups of the Primates. In the case of the lemurs the increase has been comparatively small, while in the apes and monkeys it has been relatively great.

Now, to what causes is it possible to attribute this development of the brain? A few modern naturalists of note claim to have discovered evidence of an internal perfecting or directing principle, by means of which variations along a given line only are originated and preserved, and which, through the subsequent action of natural selection, forever holds them steadfast in the narrow path of their final development. In any such view of evolution, I find it necessary to express my utter and unqualified disbelief. In my judgment, not only is there no evidence in support of such a proposition, but, on the contrary, all the facts of paleontology, as far as they are capable of any interpretation, point directly to an opposite conclusion. Such a view of evolution, moreover, presents no advantages over the antiquated doctrine of special creation, which, on account of its inconceivability as well as of total lack of evidence in its support, has long since been relegated to the category of extinct ideas.

In like manner do I find it equally difficult, and inconsistent with the evidence, to believe in the all-sufficiency of natural selection, as advocated by the Neo-Darwinian school of evolutionists. If we had no evidence other than that afforded by the well-known modifications in structure of the cave faunæ

upon which to rest our belief in certain factors concerned in evolution, we could yet feel reasonably assured that the inherited effects of disuse had played no unimportant part in the retrogressive changes which these animals have suffered in the past.

According to the very able researches of Packard and Eigenmann, the loss of sight as well as other important changes in these cave forms can be explained on no other rational hypothesis than that of *the inherited effects of disuse*; and while the admission of such explanation, as a fact, may render impossible the construction of a satisfactory theory of heredity, in the light of our present knowledge, then all that can be said is, so much the worse for a theory of heredity.* If, therefore, the inherited effects of disuse are capable of producing such profound modifications as those to which reference has just been made, it follows that the inherited effects of prolonged *use* must have been equally potent in the production of change in animal structure. This, I may say, is the kind of evolution that was taught by the great master minds who gave it birth, and, notwithstanding all the subsequent discussion which has taken place regarding the factors concerned in the process, I am still firmly of the opinion that the theory of evolution, as set forth by Darwin and Huxley, comes nearer to the truth than all others yet advanced.

With this understanding of the nature of the causes by means of which we must, in my judgment, seek to explain the progressive changes in brain structure among the Primates, we are now prepared to return to the inquiry.

It is first necessary to recall that different species of animals seem to employ the special senses in different degrees, for the purpose of acquiring information of any object that may excite their attention. Among such animals as our domestic horse and cow, if confronted by any object new or strange to them, they will at once give evidence of the fact by every attitude of marked attention. If not sufficiently frightened to run away, they proceed to inspect it from every point of vantage. Sight alone, however, seems to be insufficient to satisfy their curiosity or allay their suspicions, and it is not until they are able to approach near enough to test it fully by the sense of smell that they seem to be able to acquire the necessary information they desire. This same characteristic of depending largely upon the sense of smell is true of many animals in a state of nature. It is quite as much by this means as by the sense of sight that they detect danger.

As among the hoofed animals, the Carnivora also depend largely upon sight and smell for information. In rare instances, the dog will use his paw for the purpose of turning an object

* For the evidence in favor of the transmission of acquired characters, see also the works of Hyatt, Ryder, Cope, Beecher, and others.

over, so that he may inspect it more closely, and the raccoon and bear do this more frequently, but the lack of opposability of the thumb places great difficulties in the way of handling an object to any considerable extent.

Among the monkeys, on the other hand, information of a strange or suspicious object is obtained by sight, at first always at a respectful distance. If the animal is assured that no imminent danger threatens, he will cautiously approach for closer scrutiny; if harmless, he soon takes the object in his hands and inspects it carefully upon all sides. If there is any internal mechanism to excite curiosity, it is forthwith pulled in pieces or broken, in order that every part may be examined attentively. It is only in case of an article of food that he uses his sense of smell. In this extensive use of the hands, the monkey exhibits traits and capabilities for the acquisition of knowledge far in advance of all other mammals. Not only is there great curiosity, but an active desire for information of all things new or strange in his surroundings. The undisputed testimony of many excellent observers could be quoted in support of this assertion, but the facts are so well known that it is scarcely necessary.

That which interests us most in this connection is the extent to which the animal makes use of the prehensile extremities in acquiring information and satisfying curiosity. There can be little doubt that, as in man, the sense of sight is the source from which the greatest amount of information is derived; but at the same time the ability to pick up, handle, and closely inspect any object,—possible only with prehensile extremities,—has constituted a most powerful aid in acquiring knowledge of the smaller details. The constant action and reaction of this process, with its inherited effects, upon the brain, throughout innumerable generations, we may readily believe, have resulted in an ever widening circle of psychic activity and cerebral development.

Another factor which may have had its share in the process is the particular way in which the brain has received its supply of blood from the heart. As we have already seen, the arrangement of the entocarotid circulation is different in monkeys, apes, and man, from that found in the lemurs. In one group of the lemurs, the blood through the entocarotid is carried directly to the base of the skull, where the artery enters the middle or cerebral chamber. In another group, the blood is delivered into the posterior chamber of the skull through a foramen alongside the otic bulla, or ear pouch. In monkeys and man, the entocarotid pierces the petro-tympanic, and delivers the blood directly to the base of the brain in the middle chamber. As far as directness of supply is concerned, the

arrangement found in one section of lemurs appears to be as advantageous as that of monkeys and man, and upon any hypothesis which involves this blood supply through the entocarotids, the brain of these forms of lemur should have developed as rapidly as that of the monkeys.

The explanation of this seeming inconsistency, I apprehend, is to be found in the relative importance of the two sets of arterial feeders of the cerebral hemispheres; viz., the entocarotids and vertebrals. The latter, it should be remembered, lie deeply in the neck and pursue a somewhat tortuous course through the foramina of the neck vertebræ, finally uniting on the floor of the posterior chamber of the skull to form the basilar artery. From this trunk, a pair of arteries is given off, which diverge and pass forward along the floor of the middle chamber, to unite with the entocarotid branches, forming, in conjunction with an anterior connecting branch, the circle of Willis. From the union of the entocarotid with the anterior branch of the basilar springs a large artery which passes upward through the fissure of Sylvius, and gives the principal supply of blood to the cerebrum.

In monkeys and man, the vertebral branches are relatively small and insignificant, and the entocarotids correspondingly large. In the lemurs, on the other hand, this condition is reversed; the vertebrals are large and the entocarotids small. In the one case, the entocarotids became the predominant feeders of the cerebral hemispheres, and there was corresponding increase in size and a general increase in intelligence; in the other, this office was performed largely by the vertebrals, and the brain developed more slowly. It is evident that the advantage lay on the side of the more direct current, which must have resulted in giving a greater stimulus to the psychic activities of the monkey, and have been responsible for his evolution in this direction.

Having now stated the probable relationship which must have existed almost from the very beginning between the development of the cerebral hemispheres, the prehensile extremities, and the carotid circulation, I proceed next to an examination of the skeletal structure of the manus and pes, in which the osseous index of some of these conditions above described is plainly exhibited. Selecting one of the more typical representatives of the order, the chief osteological characters of the hand and foot may be briefly stated as follows:

The Pes.—When the four outer digits are made to rest upon a plane surface, the tibial facet of the astragalus looks almost directly inward, while the fibular facet looks upward and a little outward.* The head of the astragalus is obliquely

* These two characters do not apply to the human foot, which has been modified for terrestrial progression in the erect position.

placed and is much rounded; the tuber of the calcaneum is short and incurved; the cuboid is high, broad from side to side, and of comparatively little dorso-palmar thickness; there are never less than five digits, and with the exception of the marmosets and man, the hallux is always opposable; the metatarsals are slightly interlocking, and their distal extremities, exclusive of the hallux, display a characteristic pattern, compressed from side to side, much rounded from before backward, and with progressive disappearance of keels, grooves, and sesamoids of the flexor tendons; the phalanges are elongate and curved, and the unguals are in various stages of transition from claw to nail; the distal extremity of the metatarsal of the hallux is always provided with sesamoids, and has a distinct keel and grooves; its opposability is shown by its deeply excavated proximal extremity and the convex surface of the internal cuneiform, and its terminal phalanx is always flattened and nail-like.

The Manus.—The manus has the power of complete pronation and supination; the carpus is relatively high and narrow, and its proximal articular surface is much arched from side to side; the unciform and magnum have great relative height, and a centrale may or may not be present; the metacarpals have characteristic globular extremities, in which the keels, grooves, and sesamoids are little developed, and disappear completely in the higher forms; the phalanges are elongate, and the unguals may be compressed and clawlike or depressed and nail-like; the pollex is very generally present and, with the exception of the marmosets and some lemurs, is always opposable and nail-bearing; its opposability, like that of the hallux, is indicated by the character of its articulation with the trapezium.

The chief characters of the other parts of the skeleton are the following: The teeth have brachyodont crowns with low rounded cusps; the incisors are very generally reduced to two above and below, but exceptionally may be two above and one below (*Tarsius*), or, again, one above and below, with rodent-like modification (*Mixodectes*, *Microsyops*, *Metacheiromys*, and *Cheiromys*); the premolars rarely become molariform, but progressively decrease in number to two above and below; the orbit, except possibly in a few instances, is always encircled by bone posteriorly, the orbital and temporal fossæ are separated by a bony partition in the higher forms, and the eyes are directed forward; the mandibular rami are early coössified in the more advanced species; the limbs are elongate and well developed, and clavicles are always present; the coracoid is large, the olecranon is short, and the fibula is very generally unreduced; the astragalus is without an astragalar foramen.

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XV, MAY, 1903.]

CLASSIFICATION OF THE PRIMATES.

IN dividing this order into its primary branches, the first and most necessary step is to obtain, if possible, a clear and comprehensive understanding of the essential or fundamental features which characterize the several lines upon the basis of their evolution. It is naturally to be expected, that, as we approach the point of common origin, these features will become less and less accentuated, and those characters which in the final development have become most pronounced, will be found to be inconspicuous and apparently of little significance in the beginning.

It should be also remembered, that, while some of the phyla have progressed along the lines of their final development with comparative rapidity, and have modified many of the characters which were more or less common to all Primates in the earlier stages of their history, others have retained the primitive features to a greater or less extent. Thus, the presence of such characters as an increased number of premolars, the tritubercular condition of the molars, the small size of the cerebral lobes, with the greater or less development of their several parts, the presence of a floccular fossa of the skull, a third trochanter of the femur, or an entepicondylar foramen of the humerus, the possession of claws instead of nails on the terminal phalanges, as well as many other similar characters, are to be looked upon as common primitive features which characterize all early Primates. Any one of the phyla may have separately and independently modified these features according to the requirements of a new environment.

As an example in illustration of this statement, one might meet with a Primate in which the premolars were much reduced in number, in which the molars were fully quadritubercular, the face much shortened, the brain highly developed, the temporal and orbital fossæ separated by a bony plate; in short, in which might be found many of the characters of the most highly developed Primates; but if, at the same time, the specimen exhibited the peculiarities of the incisors, canines, and the caniniform lower premolar, as well as the cerebral circulation characteristic of the lemurs, one could be perfectly certain that the species was genetically related to and belonged in the Lemuroidea and was not a

member of the Anthropoidea.* We therefore finally come to learn what the essential or fundamental characters really are, and in proportion as our knowledge increases in this direction, in just that proportion shall we be able not only to arrange the species, genera, families, etc., in their true and proper relations to each other, but at the same time may feel assured that such an arrangement represents something more than a mere convenience.

As long as we hold fast to the old horizontal system, our classification will be artificial and unsatisfactory. This is nevertheless oftentimes necessitated by our lack of knowledge, but whenever evidence from the extinct forms is to be had, sufficient to furnish even an incomplete glimpse at the phyletic history, we shall always obtain much more satisfactory results by arranging our classification accordingly. It is by reason of this increase in our knowledge of extinct forms that frequent innovations are necessary, in order to give some expression to the general affiliations which the new discoveries reveal. Our knowledge of the more exact relationships of the various representatives of the Primates is still far from complete, yet I am persuaded that a considerable advance over the older conceptions is now not only possible but urgently demanded. The classification herein proposed introduces some novel features, which may or may not stand the test and be justified by future discovery, but it none the less denotes an effort to give expression to some of the genetic affinities of the several known types of the order, which a study of the extinct forms reveals.

It has been customary to include among the Primates the North American Hyopsodidæ, a small family containing two genera and some four or five species, which are limited in their vertical distribution to the Middle and Upper Eocene strata. Hitherto, nothing has been known of the skeleton, and consequently they have been placed in various positions within the order. In the skull, of which a fairly complete specimen was found by me in the Washakie Basin, Wyoming, in 1895, and is now preserved in the collections of the American Museum, there is no ossified tympanic bulla, and the carotid canal enters the cranium as in the Insectivora. The *foramen ovale* is placed well within the alisphenoid, and is not a notch

* Such an example was, in fact, an actual occurrence. Dr. Forsyth Major discovered an extinct Primate in Madagascar, which he named *Nesopithecus*. From the unusually high development of the skull, and its many resemblances to the higher apes, he concluded that it was an Anthropoid. Lydekker, however, justly criticised this view, and pointed out that, owing to the distinctly lemurine character of the incisors and the caniniform enlargement of the first lower premolar, it should be classed as a highly developed Lemuroid.

in its posterior border completed by the periotic, as is so frequently, if not universally, the case in the lemurs. The incisors are three above and below, and the lachrymal canal is located within the orbit. Although not positively known, it is probable that the lachrymal did not have an extraorbital extension. The pattern of the molars is unlike that of any known Primate, but in many respects is like that of certain primitive Ungulates. From several fragmentary skeletons in the Marsh collection, I am now fortunately able to state that the limbs were totally unlike those of the Primates. In the presence of a supertrochlear foramen, the humerus differs from that of any known Primate. The metapodials do not display the typical globular heads of those of the Primates, but are depressed and strongly keeled at their distal ends. The phalanges are short and stout, and give to the foot a distinctly terrestrial rather than an arboreal character; and, lastly, may be noted the very important character of a completely nonopposable hallux. The North American Hyopsodidæ do not, in fact, possess a single Primate feature, as far as can be discovered, but on the contrary are much more like the Insectivora, to which order I refer them. A summary of the foregoing characters, in which they differ from typical Primates, may be given as follows:

(1) There are three incisors above and below; (2) there is no ossified tympanic bulla; (3) the structure of the molars is not like that of the Primates; (4) the entocarotid circulation is like that of the Insectivora; (5) the limb bones differ from those of any known Primate; (6) the metapodials are not Primate; (7) the phalanges are short; and (8) the hallux is not opposable.

It would appear from the evidence obtained that there are no less than three distinct primary divisions of the order now known, and as these represent as many subordinal groups, the Primates have accordingly been divided into three sections.

The first group which is deserving of a subordinal rank among the Primates, although not commonly admitted, is that represented by the living Aye Aye of Madagascar. Along with this go the American Eocene genera *Mixodectes*, *Cynodontomys*, *Microsyops*, *Smilodectes*, and *Metacheiromys*. The most distinctive and important features of this group consist in the enlargement of the central pair of incisors, the limitation of the enamel to their anterior faces in the later forms, in consequence of which they wear into chisel-shaped points, and, finally, their growth from persistent pulps. Concomitantly, the outer incisors and canines disappear, and the mandibular condyles as well as the glenoid fossæ become modified and adapted to a longitudinal, instead of a vertical

movement of the lower jaw, as in the Rodentia. The entocarotid circulation in *Cheiromys* is like that of the lemurs; the lachrymals are large, with extraorbital extension, and the external opening of the lachrymal canal is outside of the orbit. As in the lemurs, the lachrymal and malar are in contact. *Cheiromys* also agrees with the lemurs in having the fourth digit of the manus the longest of the series, and, except for the hallux, the terminal phalanges are clawlike. In all, there is a well-ossified tympanic bulla, and the limbs and feet are elongate and fully adapted to arboreal life.

Owing to the wide separation both in time and space, it has been doubted whether there is any genetic connection between the aberrant Madagascar species and the extinct North American forms. Indeed, Osborn has recently placed the American series in a primitive suborder of the Rodentia, which he calls the Proglires. After a careful investigation of the evidence, I do not hesitate to state it as my belief that the Madagascar and American forms are intimately related. There can be no two opinions respecting the Primate affinities of *Cheiromys*. This has long since been settled beyond all dispute, and although but comparatively little of the skeleton of the American species is known, what is known betrays the same Primate stamp with equal distinctness. In the New World forms, we have the following conditions presented: Ancient primitive Primates undergoing a rodent-like modification of the central pair of incisors, together with the disappearance of the outer pair and the canines. In American genera, the process is progressive but incomplete, while in the living Madagascar species the modification is complete. No stronger general argument, it seems to me, could be put forth in favor of their relationship, especially when it is remembered that these are the only representatives of the Primates in which the slightest tendency toward such modification is shown. That so distinctive and profound a change could have originated twice independently, in the same order, is so highly improbable as to be unworthy of serious consideration. That the group is of pre-Tertiary origin is shown by the fact that *Mixodectes*, its oldest representative, is already highly modified in the Torrejon or second stage of the Lower Eocene. I propose for the suborder the slightly modified term *Cheiromyoidea*.

The second suborder of the Primates includes the lemurs, a group which has long been recognized by zoologists as constituting a primary division of the order. Some authorities are inclined to deny the genetic connection of this group, as well as that of the *Cheiromyoidea*, with the true monkeys, and assign to them a separate and independent ordinal rank. This,

however, is manifestly incorrect, as all the evidence from both living and extinct forms tends to show.

Their chief characters derived from the skeleton are the following: Like the preceding group, the main entocarotid does not enter the tympanic chamber; the lower incisors and canines, when present, are much compressed laterally, elongate, and procumbent in position; the first lower premolar is commonly enlarged, and functions as a canine; there is a well-ossified tympanic bulla; the fourth digit of the manus is the longest of the series; the lachrymal is very generally enlarged, with extraorbital extension, and the external opening of the lachrymal canal is always upon the outside of the orbit;* the lachrymal and malar are nearly always in contact.

Just what value is to be attached to the placentation, in estimating affinities, is a question difficult to decide, but it is believed, and strongly argued by some, that the lowly organized structures and generalized condition by means of which the foetal envelopes develop a connection with the lining membrane of the uterine walls during gestation furnish a sufficient reason for removing the lemurs widely from the monkeys. In like manner, the rudimentary condition of the posterior cornu and hippocampus minor of the cerebrum, as well as the convolution of the transverse colon, have been looked upon as characters of great significance in classification. While it is probably true that these characters derived from the soft anatomy indicate a wide distinction between existing monkeys and lemurs, yet it is much to be doubted whether these distinctions would not assume very small proportions, or completely disappear, did we have an Eocene monkey with which to make the comparison.

Touching the question of the value of the manner of placentation as applied to the classification of the Mammalia, it is well to recall the words of Flower and Lydekker on this topic. In speaking of the "deciduate" and "non-deciduate" varieties of placenta, they say:† "It was once thought that the distinction between those two forms of placentation is so important as to constitute a sufficiently valid basis for a primary division of the placental mammals into two groups. It has, however, been shown that the distinction is one rather of degree than of kind, as intermediate conditions may exist, and it is probable that in different primary groups the simpler, non-deciduate form may have become developed independently into one or other of the more complex kinds. * * * * * We may conclude

* An exception to this last statement is found in the extinct Malagassy lemur *Nesopithecus* of Forsyth Major. In this species, according to its describer, both the lachrymal and the lachrymal opening are within the orbit.

† Mammals, Living and Extinct, 1891, p. 80.

that, although the characters and arrangement of the foetal structures may not have that extreme importance which has been attributed to them by some zoologists, they will form, especially when more completely understood, valuable aids in the study of the natural affinities and evolution of the Mammalia."

In view of the important fact that the soft anatomy of extinct forms is wholly inaccessible and will remain forever hidden from us, and furthermore, not knowing exactly what value to attach to characters derived from this source among living forms, it seems by far the safest plan to rely largely, if not solely, upon osteological evidence for our conclusions respecting the affinities and evolution of the various groups of the Mammalia. The facts afforded by the skeleton are the only ones whereby we are permitted to make a direct comparison between the structure of living and extinct forms, and should, therefore, always be ranked as of the first importance.

The following are the chief primitive characters of the lemuroid skeleton: The cranial cavity is proportionately small; the face is generally large and elongate in comparison with the size of the brain case; the temporal and orbital fossæ are not separated by a bony plate (except in *Nesopithecus*); the zygomata are usually broad and heavy, and the malar frequently extends beneath the zygomatic process of the squamosal to near the glenoid fossa, as in the Marsupials; the malar articulates with the lachrymal in front in many species, thereby shutting out the maxillary from a share in the anterior or lower rim of the orbit; there is usually a considerable interorbital breadth; the squamosal has little vertical expansion on the side wall of the skull; there are nearly always large postglenoid foramina; the posterior free edge of the hard palate is thickened; the molars are for the most part tritubercular; the atlas has separate openings for the two divisions of the suboccipital nerve; the ilium is generally little expanded; the head of the femur is more or less sessile upon the shaft; the digital fossa has a slitlike form; the second trochanter is large and internal in position, and there is always a third trochanter; the proximal plantar extremity of the metatarsal of the hallux, for the attachment of the long peroneal tendon, is enlarged and prolonged; the second digit of the pes bears a terminal claw, and the humerus has an entepicondylar foramen.

It is at present difficult to decide just how many families should be recognized in this suborder. A conservative estimate would not place them above two or perhaps three. Of these, the living species would constitute one, the Lemuridæ; the extinct Malagassy *Nesopithecus* a second, the Nesopithecidæ, and very doubtfully the extinct *Megaladapis* a third, the

Megaladapidae. It should be remembered, however, that the Lemuridae, as thus constituted, include forms of very diverse structure and probably not very closely related. Thus the Indrisinae, usually considered as one of the best-marked and most distinct subfamilies, in the absence of one pair of incisors or canines in the lower jaw, together with the strongly developed mesostyle of the superior molars, appear to be sufficiently differentiated from the central forms of the typical lemurs to be entitled to a distinct family rank.

The third and last primary division of the order is the Anthropoidea, and in the present state of our knowledge it seems quite impossible to obtain any very clear insight into the phyletic history of the various groups composing it. Until much additional information is secured concerning many of the fossil types already known, as well as of the large number of undiscovered connecting forms which must have certainly existed, any attempts at a classification that may be regarded as final can not at present be made. Still, certain advance steps may, I think, now be taken, which will help considerably toward a final solution of some of the many difficult problems involved in unraveling the tangled web of simian evolution.

The characters by means of which the members of the group are distinguished from the two foregoing suborders are as follows: Incisors reduced to two pairs above and below (in *Tarsius*, one below); they have a normal form and position; there is no caniniform enlargement of the first lower premolar; the entocarotids traverse the petro-tympanic; the lachrymal canal (except in one group) is more or less confined within the orbit, and the facial part of the bone is quite generally reduced; the lachrymal and malar are not in contact, leaving the maxillary a share in forming the anterior rim of the orbit; the fourth digit of the manus is never the longest of the series.

It would appear from present evidence that the Anthropoidea early divided into at least three main branches, but the exact lines of descent from these starting points can not now be traced with any degree of certainty, among the majority of the living species. The first of these divisions is represented by the living marmosets, a group which Huxley classified under the name of the Arctopithecini.* Their chief claim to distinction consists in the lack of opposability of the hallux and pollex; the clawed condition of all the terminal phalanges of both manus and pes, except a slight flattening of that of the hallux; the loss of the third molar above and below, and the tritubercular condition of the superior molars. These characters, except the last, are unique among the Primates, and may or may not indicate a very ancient branching from the main

* Anatomy of Vertebrated Animals, 1872, p. 392.

axis. Whatever classification is finally adopted, it seems to me that this should be regarded as one of the primary divisions of the suborder, since the characters of the extremities are not found in any other member of the order thus far known.

In the second division of the Anthropeidea, I included *Tarsius* and its allies. It has been customary with nearly all authorities to classify this species in the Lemuroidea, assigning to it the rank of a separate and distinct family. Hubrecht,* however, from a careful study of its placentation has shown that in this respect it is widely different from the lemurs and decidedly like the monkeys. Hence, he has proposed its removal to the Anthropeidea. In confirmation of this view, it may be added that the entocarotid circulation, which I am inclined to regard as of fundamental importance, is analogous to that of the primitive monkeys and not like that of any of the lemurs. Similarly, the lack of union between the malar and lachrymal is found in all the monkeys, and the reverse condition in the lemurs. The teeth do not exhibit that peculiar modification seen in all lemurs, but again are like those of the monkeys; and, lastly, the fourth digit of the manus is not the longest of the series as in all the lemurs, but is shorter than the third as in the monkeys. Thus, it will be seen that the evidence derived from five independent sets of organs, the placentation, lachrymo-malar union, entocarotid circulation, dentition, and digital lengths of the manus, all concur in assigning to *Tarsius* a position with the monkeys and not with the lemurs. On the other hand, it may be stated that in the extraorbital extension of the lachrymal and the location of the external openings of the lachrymal canal outside the rim of the orbit, it agrees with the lemurs.

This question of the lachrymal region in the skull of the Primates has recently formed the subject of extensive and painstaking research by Forsyth Major.† From his investigations, we learn that, with the single exception of *Nesopithecus*, a highly developed extinct type from Madagascar, all the lemurs possess an enlarged lachrymal which reaches beyond the orbit, while the external opening of the lachrymal canal is situated upon the side of the face. In some species, notably *Loris*, no lachrymal was found, but there can be little doubt that its absence is due to early fusion with the maxillary and complete obliteration of the sutures, as in the sea-lions and seals. Another interesting observation recorded by Dr. Major relates to the lachrymal enlargement seen in certain South

* Die Keimblase von *Tarsius*. Festschrift für Carl Gegenbaur, Leipzig, 1896. The Descent of the Primates, Princeton Lecture, 1897.

† On Some Characters of the Skull in Lemurs and Monkeys, Proc. Zool. Soc. London, February, 1901.

American apes, as the howlers and woolly spiders, wherein it is impossible to decide whether the lachrymal canal can be said to be within or without the orbit. In view of these transitional conditions, the great taxonomic significance of the position of the lachrymal canal, which it was formerly thought to possess, is materially weakened. The large lachrymal with the opening of the canal extraorbital in position is undoubtedly the primitive condition. This is demonstrated by reference to the Marsupials, in some of which, notably *Myrmecobius*, it is unusually large and sends a considerable spur outward upon the zygoma to join the malar. In all Insectivora, Rodentia, and primitive Carnivora, the enlarged lachrymal as well as the extraorbital position of the canal, is, as far as I am aware, universal.

For views in favor of retaining *Tarsius* in the Lemuroidea, as well as for a general discussion of the genetic relationship of the latter to the Anthropoidea, I refer the reader to the excellent papers by Mr. Charles Earle.*

If *Tarsius* is a member of the suborder Anthropoidea, of which in my judgment there can be little question, then it appears equally certain that, with its allies, it represents an independent branch from the main axis, and one, moreover, of equal rank with the Arctopithecini, or marmosets, since its primitive lachrymal arrangement associated with precocious tooth reduction, as well as with some peculiarities of the pterygoid region, mark it off distinctly as a side branch. I suggest for this group, therefore, the name Paleopithecini.

Of the extinct American types, *Euryacodon* and *Anaptomorphus* are names which probably refer to one and the same genus. The skull structure of the best-known species, *Anaptomorphus* or *Euryacodon homunculus*, was described by Cope from an exceptionally fine specimen found by me in the Wasatch bed of the Big Horn Valley, Wyoming, in 1881. This specimen has recently been refigured by Osborn.† Its resemblance to *Tarsius* is so striking that there can be apparently no question whatever of the near relationship of the two. This is seen in the following important characters: The entocarotid canal traverses the tympanic chamber, and its external orifice is situated as in *Tarsius*; the malar does not unite with the lachrymal; the lachrymal is relatively large and extends out upon the face; the external opening of the lachrymal canal is extraorbital in position; the auditory bullæ are much inflated and the external alæ of the pterygoids extend outward and backward in such a manner as more or less to enclose the bullæ; the structure of the teeth

* Science, February 12, 1897; and May, 1897. American Naturalist, July and August, 1897.

† American Eocene Primates, Bull. Amer. Mus. Nat. Hist., June, 1902.

resembles that of *Tarsius* very closely, and the premolars in the Bridger species at least are reduced to two; there is no lemurine modification of the incisors or first lower premolar; the brain is relatively large, and the face is considerably bent down on the basicranial axis, as in *Tarsius*; while, lastly, the species are small and the orbital cavities enlarged.

From this striking array of similarities which Cope was careful to point out, I am fully convinced that the two forms are closely related and should be placed in the same group. In like manner, we may feel reasonably certain in arranging the extinct European *Necrolemur* of Filhol in the same group. Although the skull characters are less perfectly known than in the American species, yet the lachrymal region, the dentition, and the general appearance of the single skull known, all betray the same fundamental resemblances to *Tarsius* noted in *Anaptomorphus* or *Euryacodon*. I do not hesitate, therefore, to classify it with this series. The same may also be true of the imperfectly known *Microchærus* of the European Eocene, but this is not at all certain. There is some evidence that the latter genus is closely related to and represents *Hyopsodus* in Europe.

The position of the remaining American genera, *Omomys*, *Hemiacodon*, and *Washakius*, is more problematical. No complete skull of any of these forms is known, and it is impossible to say whether they most resemble *Tarsius* or the monkeys. In one species, *Hemiacodon gracilis*, a fragment of the maxillary is sufficiently preserved to show that there was no union between the malar and lachrymal. The incisors do not display any lemurine characteristic and the inference is tolerably clear that they belong either with the Paleopithecini or with the true monkeys. I may add just here that there is such a marked resemblance between the teeth of *Omomys* and those of certain of the living South American Cebidæ, that I am strongly inclined to the belief that these extinct forms are true monkeys.

There yet remains to be discussed another group of extinct Primates whose remains are better preserved, and hence more completely known, than any others yet discovered in the Eocene, the Adapidæ of Europe and the so-called Notharctidæ of America. Cope* arranged them in the group Mesodonta, which he made a suborder of his order Bunotheria. He included in the Bunotheria the suborders Creodonta, Mesodonta, Insectivora, Tillodontia, and Tæniodonta, at the same time holding that the Prosimiæ, or Lemuroidea, should be placed here as well. He seems to have entertained the opinion that all were ordinarily distinct from the Quadrumana, or Primates, although

* Tertiary Vertebrata, 1884.

he does not state this directly. He defined the Mesodonta as follows: "Incisors not growing from persistent pulps; molars tubercular, never sectorial; third trochanter elevated; astragalus not grooved above." Under the head of Prosimiæ, he further adds, "The suborder may be differentiated from the Mesodonta by the possession of an opposable hallux of the posterior foot," but qualifies this definition with the statement that the lack of opposability of the hallux is not demonstrated in any of the species except *Pelycodus*.

There seems to be a great deal of confusion in Cope's statements regarding the classification of the genera under the Mesodonta and Prosimiæ. In the Mesodonta, he classified the following genera: *Omomys*, *Microsyops*, *Pantolestes*, *Tomitherium*, *Pelycodus*, *Sarcolemur*, *Hyopsodus*, *Aphelicus*, *Adapis*, and *Opisthotomus*. In the Prosimiæ, on the other hand, he included three families, viz.; Adapidæ (genera not stated), Mixodectidæ comprising the genera *Mixodectes*, *Microsyops*, and *Cynodontomys*, and the Anaptomorphidæ including *Anaptomorphus* and *Necrolemur*. It will be thus seen that several of the genera are referred to both suborders.

The next authority of note to contribute to this subject is Schlosser. He regarded all these early extinct forms as constituting a group equal in rank to that of the Lemuroidea and Anthropeidea, and one from which these two, in all probability, have been derived. This group he named the Pseudolemuroidea. Osborn in his recent paper, "American Eocene Primates,"* inclines apparently to the same view. He says: "Three suppositions are possible: First, that these Primates represent an ancient and generalized group (Mesodonta, Cope) ancestral to both Lemuroidea and Anthropeidea; second, that they include representatives of both Lemuroidea and Anthropeidea, contemporaneous and intermingled; third, that they belong exclusively to one or the other order. There are certain advantages in the revival of the term Mesodonta Cope, a suborder (anticipating the terms Pseudolemuroidea and Tarsii) which would bear somewhat the same relationship to the modern specialized Monkeys and Lemurs that the Condylarthra bear to the Ungulata and the Creodonta to the Carnivora."

As regards the validity of the group Mesodonta of Cope and its suggested revival by Osborn, very little need be said. From the most abundant skeletal materials of both *Adapis* and *Notharctus* we now know that the hallux was almost if not quite as opposable as in any living Primate. Cope's statement, therefore, of its lack of opposability in *Pelycodus*, a genus scarcely distinct from *Notharctus*, must with almost absolute

* Loc. cit.

certainly be erroneous. His technical definition of the group, moreover, as well as its dissociation from the Primates, I regard as utterly unsound, illogical, and in no wise warranted by the facts. I do not believe that any such natural group exists, and a revival of the name Mesodonta can result only in confusion. As we have already seen, there are types of very different affinities among these ancient Primates, and this fact in my judgment effectually precludes the possibility of their association into a single group. What position, then, do *Adapis* and *Notharctus* occupy with reference to these natural groups already outlined? That they can not be consistently placed in the Lemuroidea is evident for the following reasons: The incisors do not exhibit any traces of lemurine modification, but, on the contrary, are like those in typical monkeys; the main entocarotid canal traverses the petro-tympanic chamber as in *Tarsius*; the lachrymal and malar do not unite on the anterior rim of the orbit; the digital lengths of the manus are not known with certainty, but in *Notharctus*, the evidence is reasonably conclusive that the fourth was not longer than the third.

On the other hand, their resemblance to the Paleopithecini is more marked. This is seen in the greatly inflated condition of the tympanic bullæ as well as in the outward and backward extension of the external alæ of the pterygoids. These forms differ from the Paleopithecini, however, in having a more reduced lachrymal, in the position of the external opening of the lachrymal canal on or near the rim of the orbit, in having a greater number of premolars, and in general in being larger and of more robust proportions. Thus, it will be seen that they occupy a position intermediate in many respects between the remaining Anthropoidea and the Paleopithecini. In the latter, there seems to have been a marked tendency toward precocious specialization in both tooth reduction and brain enlargement, which are curiously associated with retention of the primitive condition of the lachrymal. *Adapis* and *Notharctus*, on the other hand, exhibit advance in the reduction of the lachrymals, but retain the more generalized features of the dentition and brain enlargement. These are the essential differences between the two lines and mark out very distinctly the trend as well as the possibilities of their future development. It is in just such a group as that which includes *Adapis*, *Notharctus*, and *Limnotherium*, that we must seek for the beginnings of the higher monkeys and apes which follow; and while these species, at present the only well-known types of the series, may not have been in the direct line of descent, they can not at the same time have been far removed from it. *Omomys* and *Washakius*,

as far at least as we are permitted to judge from their scant remains, are closely related to *Adapis* and *Notharctus*, but had made greater progress in the reduction of the premolars. This gives an especially monkey-like appearance, pointing particularly in the direction of certain living Cebidæ. It is probable, therefore, that all this series should be classified as primitive members of a third section of the Anthropoidea. If this last division represents a homogeneous and natural group, equivalent in rank to that of the Arctopithecini and Paleopithecini, it is deserving of a name, and I suggest for it that of Neopithecini.

A summary of the foregoing discussion of the classification of the Primates, together with the more technical definitions of the several groups, is embodied in the following statement:

Limbs elongate; with prehensile manus, and pes fully adapted to an arboreal life; incisors enlarged and in later forms becoming reduced in number and rodent-like in pattern; canines disappearing in later forms; an ossified tympanic bulla; entocarotid circulation as in the Galaginæ and Lorisinæ; three families, Microsyopsidæ, Metacheiromyidæ, and Cheiromyidæ.

Cheiromyoidea.

Limbs elongate, prehensile, and adapted to an arboreal habit; incisors of lower jaw reduced in size, pectinate, and proclivous in position; anterior lower premolar very generally enlarged and functioning as a canine; entocarotid canal not traversing the petro-tympanic; malar and lachrymal very generally in contact on anterior rim of orbit; fourth digit of the manus the longest of the series; three families, Lemuridæ, Indrisidæ, and Nesopithecidæ.

Lemuroidea.

Limbs elongate, extremities prehensile, and fully adapted to an arboreal life; incisors and canines normal in form and position; entocarotid traversing petro-tympanic; malar and lachrymal not in contact on anterior rim of orbit; fourth digit of manus shorter than third; three superfamilies or groups, Arctopithecini, Paleopithecini, and Neopithecini.

Anthropoidea.

The definitions and divisions of the superfamilies of the Anthropoidea are as follows:

Hallux and pollex of manus and pes not opposable; true molars reduced to two in each jaw; one family, Hapalidæ.

Arctopithecini.

Hallux and pollex fully opposable; three true molars; lachrymal enlarged, with well-developed *pars facialis*; lachrymal canal opening without orbit; premolars precociously reduced in highest forms; two families, Anaptomorphidæ and Tarsiidæ.

Paleopithecini.

Hallux and pollex fully opposable ; three true molars ; lachrymal reduced ; lachrymal canal opening on or inside orbital rim ; premolars progressively reduced to two in advanced forms ; brain enlargement progressively increasing in the later types ; five families. Neopithecini.

The Neopithecini are divisible into at least five distinct families of which in the living fauna three are confined to the Old World* and one to the New World. One extinct family is common to the two hemispheres, and as far as can be now ascertained from the remains, occupies a position not far removed from the common primitive stem from which the great majority of the living simian population of the Old and New Worlds originated. In the case of the Old World families, the gap is as yet very wide, but in the case of the New World Cebidæ, the interval is much less, and is not greater than one would be reasonably led to anticipate between an ancestor of Upper Eocene time and a living descendant. In fact, the difference is not nearly as great as it is between the modern horse and its Upper Eocene progenitor, *Orohippus*. As this phase of the subject will be more fully discussed in another section of the present paper, it may be here dismissed.

The families of the Neopithecini are distinguished upon osteological considerations, as follows :

Premolars four above and below ; orbital and temporal fossæ more or less freely continuous ; parietal uniting with alisphenoid on side wall of cranium ; molars more or less fully quadritubercular, with ridges of superior trigon distinct ; a large petro-tympanic bulla expanded behind ; external auditory meatus not prolonged into a tube ; carotid canal piercing bulla near postero-external angle ; a postglenoid foramen ; muzzle elongate ; lachrymal slightly extended beyond rim of orbit, with opening of lachrymal canal upon edge of orbit ; ilium little expanded ; ischium without distal enlargement or everted edges ; head of femur more or less sessile upon shaft ; digital fossa of femur narrow and slitlike ; a third trochanter and an entepicondylar foramen ; hallux fully opposable ; metatarsal of hallux with elongate proximal plantar extremity ; pollex not as fully opposable as in higher species ; foramina of atlas complex. Adapidæ.

Premolars three above and below ; orbital and temporal fossæ separated by bony plate ; parietal uniting with alisphenoid on side wall of cranium ; frontal excluded from contact with alisphenoid by malar on side of skull (except in *Mycetes* and some species of *Ateles*) ; molars fully quadritubercular, with ridges of superior trigon distinct ; first lower premolar without elongate

* In this statement, the origin of man is considered to have taken place in the Old World.

anterior border, as in preceding family; petro-tympanic bulla little expanded behind; no vaginal process; auditory meatus not prolonged into a tube; carotid canal piercing bulla near postero-internal angle; a large floccular fossa on internal surface of periotic; postglenoid foramen present or absent; muzzle abbreviated; lachrymal either slightly extended beyond rim of orbit or confined wholly within it; ilium well expanded; ischium without distal enlargement and edges not everted; head of femur with well-defined neck and an open digital fossa; no third trochanter; an entepicondylar foramen of humerus; hallux fully opposable; metatarsal of hallux without elongate proximal plantar extremity; pollex not as fully opposable as in higher species; foramina of atlas complex. Cebidæ.

Premolars two above and below; orbital and temporal fossæ separated by bony plate; no parieto-sphenoid but a temporo-frontal contact in the side wall of the cranium; frontal and alisphenoid not separated by malar on side wall of cranium; molars fully quadritubercular of squarish outline, without traces of superior trigonal ridges, but tending to the formation of cross crests; first (third) inferior premolar with characteristic elongation of anterior border; petro-tympanic bulla little inflated and filled with cancellous tissue; no vaginal process; auditory meatus prolonged into a bony tube; carotid canal piercing bulla near postero-internal angle; a large floccular fossa on inner surface of periotic; presphenoid and basisphenoid remaining long distinct, as in preceding family; no postglenoid foramen; muzzle abbreviated; lachrymal never reaching rim of orbit, and of much greater vertical than transverse extent; ilium well expanded; ischium with distal enlargement and everted edges; head of femur with well-defined neck and an open digital fossa; no third trochanter; no entepicondylar foramen of humerus; hallux fully opposable; metatarsal of hallux without elongate proximal plantar extremity; pollex fully opposable; foramina of atlas complex or simple. Cercopithecidæ.

Premolars two above and below; canines enlarged and of greater vertical extent than premolars and incisors, as in preceding families; orbital and temporal fossæ distinct; a temporo-frontal contact on side wall of skull (except in Orang); frontal and alisphenoid not separated by malar on side wall of cranium; molars fully quadritubercular, with more or less rounded outline, without any tendency to the formation of transverse crests, but with distinct remains of superior trigonal ridges; first (third) inferior premolar with traces of elongate anterior border (least distinct in Chimpanzee); petro-tympanic bulla little inflated, with a moderately well-developed vaginal process (except in *Hylobates*) and no ossified styloid process as in preceding families; auditory meatus elongate; carotid canal as in Cercopithecidæ; floccular fossa on internal surface of periotic vestigial;

no postglenoid foramen; presphenoid and basisphenoid early coössified; lachrymal confined within the orbit, having a quadrate outline without vertical enlargement (except in *Hylobates*); ilium expanded; ischium with only moderate distal enlargement and without strongly everted edges (except in *Hylobates*); head of femur with well-developed neck and open digital fossa; no third trochanter; no entepicondylar foramen; hallux and metacarpal of hallux as in *Cercopithecidae*; pollex fully opposable; sesamoids of flexor tendons of four outer digits in manus and pes vestigial or wanting and keels absent (except in *Hylobates*); foramina of atlas simple; as in the preceding families, the mastoid process is rudimental or wanting and the premaxillo-maxillary suture long persists, being obliterated only in aged specimens; there is no foramen spinosum for the passage of the middle meningeal artery, but a notch in the anterior external part of the foramen ovale apparently represents it in the Gorilla and Chimpanzee; the frontals meet in the middle line over the presphenoid and behind the ethmoid (except in Orang). Simiidae.

Premolars two above and below; canines reduced and of no greater vertical extent than premolars and incisors; orbital and temporal fossæ distinct; a spheno-parietal contact on the side wall of cranium (variable); frontal and sphenoid not separated by malar on side wall of skull; molars fully quadritubercular with superior trigonal ridges distinct; first (third) inferior premolar without any trace of elongate anterior border; no petrotympanic bulla; but a well-defined vaginal process and a well-ossified and coössified stylohyal; external auditory meatus and carotid canal as in *Simiidae*; no postglenoid foramen; no floccular fossa on inner surface of periotic; presphenoid and basisphenoid early coössified; lachrymal confined within the orbit, having a much greater vertical than antero-posterior diameter; distal enlargement of ischium reduced and edges not everted; neck of femur and digital fossa as in *Simiidae*; hallux enlarged, not opposable and in line with other digits; keels, grooves, and sesamoids of four outer metapodials of manus and pes absent; foramina of the atlas simple; a well-developed mastoid process; the maxillo-premaxillary suture early obliterated; a distinct foramen spinosum for the passage of the middle meningeal artery; no union of frontals over presphenoid and behind ethmoid. Hominidae.

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XV, JUNE, 1903.]

Origin of the Primates.

IN any attempt at a consideration of the question of the origin of the Primates, we are met almost at the very threshold of our inquiry by such a lack of definite information as effectually to bar our progress, in so far, at least, as positive or decided results are concerned. The only course that is open to us at present is to reason by induction and analogy, but it may well be that this method will prove futile enough and furnish a very unsafe guide in threading our way across this unexplored waste in the knowledge of simian history.

The first question of importance to discuss in this connection is the probable location of the place of origin of the Primates, and just here some welcome facts come to our aid. From the abundant and well-attested records of paleobotany, we learn first of all that a tropical vegetation flourished within the Arctic Circle as late as the beginning of the Cretaceous, and for reasons which will be presently given it appears highly probable that this was one of the regions in which climatic environment first presented sufficiently favorable conditions for the beginnings of higher forms of plant life. In other words, it was probably the original home of the Angiosperms, or flowering plants. The existence of the higher types of Mammalia was manifestly impossible before the appearance of the necessary plants upon which they so largely depend for food, and I shall therefore assume the existence of a close and intimate relationship between the development of the one and the origin of the other.

Just what climatic conditions obtained in the polar regions prior to the Cretaceous, whether there were alternate periods of heat and cold with consequent glaciation, or whether the climate was uniformly tropical, are questions with which our present inquiry is not vitally concerned, for the reason that the origin of the higher forms of mammalian life can not be consistently placed at a much earlier date than the beginning of the Cretaceous.

Touching the question of former glacial epochs, however, it is proper to state that more recent geological investigations have shown the existence of boulders of great size and thickness, scratched and glacial-like, in beds of Permian and probably of Triassic age also, in Australia, New Zealand, South Africa, India, and presumably in South America. The wide-spread occurrence of these phenomena over the Southern Hemisphere would seem to be impossible of explanation on any hypothesis other than that of glaciation or a period of cold. Such facts have led many geologists to believe in the existence of successive or intermittent glacial epochs in the past. A fair estimate of present opinion on the subject may be gained from Dana's statement,* which is as follows: "Thus, throughout the earth's history since life began, the only cold epochs of which proof has been found occurred near or at the close of the Permian, at the close of the Triassic, and during the Glacial period. At the close of the Cretaceous, another epoch is suspected to have occurred, but without direct evidence."

With a few exceptions the evidence of glaciation in the Northern Hemisphere is confined almost exclusively to the Glacial epoch proper, and it is to be seriously doubted whether conclusive proof of wide-spread glacial action in any former period will ever be found. At all events we are not warranted in the belief that a frigid temperature overspread the Northern Hemisphere at any time between the Jurassic and the Tertiary. On the contrary, all the testimony which has yet been gathered from various available sources shows that there were slow and gradual changes of temperature from tropical, through all the stages of subtropical, warm temperate, temperate, cold temperate, subfrigid, and frigid, in the long interval between the Jurassic and the Glacial epochs.

The class of facts upon which we most largely depend for conclusions respecting the former climatic conditions in any region are furnished by the fossil remains of plants and animals imbedded in its strata. In order that evidence of this character may become available, we must assume two propositions: (1)

* *Manual of Geology*, 1894, p. 1027.

That the animals and plants lived and died in the vicinity where their fossil remains occur; and (2) that by comparison with their nearest living allies we may deduce some information respecting their habits. For example, we know that such plants as Palms, Cycads, and Tree-Ferns require a given mean temperature for their existence. Frost quickly destroys them and they rapidly disappear where much freezing takes place. Their northernmost limit is found, therefore, at or near the isothermal line separating a warm temperate from a subtropical temperature. Thus, while a few of the hardier forms may be distributed along the borders, the vast majority of the species inhabit the more central tropical and subtropical parts of the earth, where they form a conspicuous and characteristic feature of the flora.

If, therefore, the remains of such forms as Palms, Cycads, or Tree-Ferns occur as fossils in a given locality, we may conclude without fear of error that the temperature of such place could not have been below that which at present limits their distribution, yet it may at the same time have been tropical or subtropical. Some information regarding the latter condition may be had from the relative abundance of remains of such species. If very abundant and in considerable variety, a subtropical or tropical temperature rather than that bordering on a warm temperature would be indicated. In the same way, we may assume the presence of remains of certain species of extinct animals to be indicative of, and equally conclusive proof of, temperatures in which their nearest allies live at the present day.

With this understanding of the nature of the evidence upon which we must rely, I pass next to a brief review of the former distribution of the plants in the Northern Hemisphere, and shall begin with a consideration of the fossil floræ of the Arctic regions. Certain deposits in Greenland, near Disco Island, $70^{\circ} 33'$ N. Lat.—the Komé beds—have yielded a rich flora, which according to Heer, its describer, is strictly comparable with that of the Neocomian or Lower Cretaceous of Europe and America. It includes Ferns, Cycads, Conifers, and a single species of Angiosperm—a Poplar. Of the Ferns, the genus *Gleichenia*, now almost exclusively tropical in its distribution, is represented by fifteen species. There are also four genera of Cycads, with numerous species, whose nearest living representatives now inhabit the tropical and subtropical regions. Pines, Redwoods, and other Conifers, some closely related species to which are now found living in China and California, go to make up the list of the Gymnosperms. The Angiosperms, as far as we now know, are represented by the single genus and

species *Populus primæva*, which is probably the oldest Angiosperm thus far discovered.

In such distant localities within the Polar regions as Spitzbergen and Alaska are found deposits of nearly or quite the same age, and here the same or a closely allied flora occurs. The conclusion is therefore obvious that the climatic conditions by which this plant life was surrounded were not confined to a single locality and were not the result of local changes, but this evidence compels us to believe that they were widespread and general over the whole Arctic region during this period. The mean temperature indicated by these plants, according to Heer,* than whom no better authority could be quoted, was from 21° to 22° C., or 70° to 72° F. This brings it very near the isothermal line 74° F., which separates the subtropical from the tropical temperature; hence the climate may be said to have been virtually tropical.

Deposits corresponding closely in age to that of the Upper Cretaceous of Europe and North America are found in the same latitude, near the same locality as that just described. These beds—the Atané—have furnished the remains of a flora no less remarkable than that of the Lower Cretaceous. In all, sixty-five species have been identified, of which fifteen are Ferns, two Cycads, eleven Conifers, three Monocotyledons, and thirty-four Dicotyledons. Of the Ferns, one is a Tree-Fern, which, with the Cycads and other species, at once gives a subtropical aspect to the flora. The Dicotyledons include such types as the Poplars, Bayberry and Sweet Fern, Fig, Sassafras, Heath, Cinnamon, Persimmon, Aralia or Ginseng, Magnolia, Myrtle, and Legumes. The living representatives of many of these species are now found in a subtropical or warm temperate climate, and if such evidence has any value it furnishes incontestable proof that the temperature of the Arctic regions, although still tropical, had suffered a decline from that of the Lower Cretaceous during the latter part of the period.

Turning next to the Tertiary, we find from the same class of evidence that wide-spread changes in the climatic conditions had occurred. There are deposits at many localities within the Arctic regions in which plant remains of this epoch are found, but their exact equivalents among European and American beds are difficult of determination. They were referred by Heer to the Miocene, but Dawson expressed the opinion that they were at least in part Eocene in age—a view which is more likely the correct one. Further exploration and the discovery of animal remains are necessary before these matters can be finally cleared up. At all events, it is perfectly

* See Professor Heer's famous work, *Flora Fossilis Arctica*.

certain that they are later in age than those containing the Upper Cretaceous flora above described.

As Wallace gives such an excellent summary of what is known on this subject, I quote his statement in full. He says :*
“ One of the most startling and important of the scientific discoveries of the last forty years has been that of the relics of a luxuriant flora in the various parts of the Arctic regions. It is a discovery that was totally unexpected and is even now considered by many men of science to be completely unintelligible ; but it is so thoroughly established, and it has such a direct and important bearing on the subjects we are discussing in the present volume, that it is necessary to lay a tolerably complete outline of the facts before our readers.

“ The Miocene flora of temperate Europe was very like that of Eastern Asia, Japan, and the warmer part of Eastern North America of the present day. It is very richly represented in Switzerland by well preserved fossil remains, and after a close comparison with the flora of other countries Professor Heer concludes that the Swiss Lower Miocene flora indicates a climate corresponding to that of Louisiana, North Africa, and South China, while the Upper Miocene climate of the same country would correspond to that of the south of Spain, Southern Japan, and Georgia (U. S. of America). Of this latter flora, found chiefly at Eningen in the northern extremity of Switzerland, 465 species are known, of which 166 species are trees or shrubs, half of them being evergreens. They comprise sequoias like the Californian giant trees, camphor-trees, cinnamons, sassafras, bignonias, cassias, gleditschias, tulip-trees, and many other American genera, together with maples, ashes, planes, oaks, poplars, and other familiar European trees represented by a variety of extinct species. If now we go to the west coast of Greenland in 70° N. Lat. we find abundant remains of a flora of the same general type as that of Eningen but of a more northern character. We have a sequoia identical with one of the species found at Eningen, a chestnut, salisburia, liquidambar, sassafras, and even a magnolia. We have also seven species of oaks, two planes, two vines, three beeches, four poplars, two willows, a walnut, a plum, and several shrubs supposed to be evergreens ; altogether 137 species, mostly well and abundantly preserved !

“ But even further north in Spitzbergen, in 78° and 79° N. Lat. and one of the most barren and inhospitable regions on the globe, an almost equally rich fossil flora has been discovered including several of the Greenland species, and others peculiar, but mostly of the same genera. There seem to be no evergreens here except coniferæ, one of which is identical with the

* *Island Life*, 1892, p. 183.

swamp-cypress (*Taxodium distichum*) now found living in the Southern United States! There are also eleven pines, two *Libocedrus*, two sequoias, with oaks, poplars, birches, planes, limes, a hazel, an ash, and a walnut; also water-lilies, pond-weeds and an iris—altogether about a hundred species of flowering plants. Even in Grinnell Land, within $8\frac{1}{4}$ degrees of the pole, a similar flora existed, twenty-five species of fossil plants having been collected by the last Arctic expedition, of which eighteen are identical with the species from other Arctic localities. This flora comprised poplars, birches, hazels, elms, viburnums, and eight species of conifers, including the swamp cypress and the Norway spruce (*Pinus abies*), which last does not now extend beyond $69\frac{1}{2}^{\circ}$ N.

“Fossil plants closely resembling those just mentioned have been found at many other Arctic localities, especially in Iceland, on the Mackenzie River in 65° N. Lat. and in Alaska.”

Thus it will be seen that proof in favor of the view that the Arctic regions enjoyed a mild and equable climate unbroken by periods of cold, up to and including the middle of the Tertiary, is simply incontestable and overwhelming. At the same time it is equally evident that while capable of supporting a luxuriant vegetation up to this period, the temperature, as indicated by the fossil plants, shows unmistakable signs of a slow and steady decline from a tropical to a temperate condition.

Let us next examine the evidence afforded by the plants as indicative of former climatic conditions in the regions now embraced within the North Temperate zone. Roughly speaking, we now transfer our attention some two thousand miles to the southward of these more typical localities in Greenland which have furnished the remains of the remarkable flora here discussed. Owing to more favorable circumstances and better facilities, the deposits in these latitudes have been much more extensively and thoroughly examined and their fossil contents more carefully collected and studied, than those of the Arctic regions. Moreover, we have in these deposits the remains of large numbers of extinct animals often associated with those of the plants, so that we are enabled to get a somewhat clearer idea of its ancient physical conditions. But in attempting to correlate the results of investigation obtained in one region with those in another, we have constantly to bear in mind the difficulties which beset the problem of establishing equivalency in the time scale in deposits of widely separated localities. We are accustomed to depend very largely, if not solely, upon the fossil contents of any two given strata for our ideas respecting their equivalency in age. It has no doubt often happened, however, that certain types of plants or animals originating in

one region were gradually distributed to others by migration, so that the deposits containing them would show the same or closely allied species in practically the same stages of development; yet this similarity in the contained fossils may not of necessity imply absolute synchronism of deposit, since a certain length of time must have been required for the migration, which would have been longer or shorter in proportion as the distance was great or small and the obstacles to be overcome were easy or difficult. It is just such complications as these that arise when we compare the deposits of the Arctic with those of the Temperate latitudes, and prevent a final and absolute determination of their exact equivalency.

In the North Temperate regions, the Mesozoic strata reach a high degree of development and in many places contain rich deposits of fossils. In Europe, the Triassic and Jurassic are much better developed than in America, while on the other hand the Cretaceous series is much more varied and extensive in America than in Europe.

The Jurassic of Europe has furnished a flora consisting of Conifers, Cycads, Ferns, Equiseta, and two Monocotyledons. In all, there are some one hundred and fifty species, of which over eighty are Ferns, twenty are Conifers, and thirty or forty are Cycads. The Conifers are represented by genera and species closely allied to the Yew, Pine, Arbor-Vitæ, Cypress, and Norfolk Island Pine. The two Monocotyledons are said to belong to the Arum and Pandanus families, or such types in our living flora as the Calla, Skunk Cabbage, and the Screw Pine. There are no Dicotyledons or higher Angiosperms known with certainty.

In America, the flora of the Jurassic is not so well represented, but the known species have a close relationship with those of the Jurassic of Europe. Thus, Conifers, Cycads, and Ferns are the only forms yet brought to light. The American Jura has hitherto furnished no Monocotyledons, and as in Europe, the Dicotyledons are completely absent. According to all authorities, the climatic conditions indicated by this flora, as well as by the associated animals, both Invertebrates and Vertebrates, are such as are now found in the vicinity of the Equator.

The Lower Cretaceous of Europe is well developed and in many places is capable of division into a number of substages. In England, the deposits belonging in this series are the Wealden, Lower Greensand or Aptian, and the Gault or Albian. In Portugal, at least six divisions are recognized, which correspond almost exactly with the subdivisions of the Potomac formation on the Atlantic border in this country. The flora of the Wealden, according to Ward, contains eighty species,

which include two Algæ, two Fucoids, one Hepatic, one Chara, three Equiseta, twenty-three Ferns, twenty-one Cycads, twenty-four Conifers, and one Monocotyledon. It is remarkable for the entire absence of Dicotyledons. The lowermost Cretaceous beds of Portugal, which are considered to be equivalent in age to the Wealden, have, according to the same authority, yielded two Algæ, two Hepatics, three Lycopods, two Equiseta, seventy-nine Ferns, fifteen Cycads, twenty-nine Conifers, sixteen Monocotyledons, forty-seven Dicotyledons, five anomalous types classified as Proangiosperms, and three forms of uncertain reference. In like manner, the Potomac formation of America contains Ferns, Cycads, Conifers, Monocotyledons, and Dicotyledons, in nearly the same proportion as the beds of Portugal. The character of this flora gives unmistakable evidence of a tropical climate, and while we are not able to say whether the temperature was actually higher than in Greenland during the deposition of the beds supposed to be of the same age, we may feel perfectly certain that tropical conditions were wide-spread over the Northern Hemisphere during the early part of the Cretaceous.

In the basal strata of the Lower Cretaceous, no remains of true Dicotyledons have as yet been found. Higher up in the series they occur sparingly, but toward the top of the section they suddenly appear in great numbers and variety. Thus, in the Gault of England and in beds of corresponding age in Portugal are found the leaves of Poplar, Magnolia, Myrtle, Willow, Walnut, Maple, Sassafras, Fig, Cinnamon, Holly, Oak, Redwood, and Palms. In America, in beds of approximately, if not identically, the same age, occur Sassafras, Tulip-Tree, Magnolia, Aralia, Cinnamon, Poplar, Willow, Maple, Birch, Chestnut, Alder, Beech, Elm, Sequoias, and Palms, the leaves of some of the latter being ten feet in diameter. The leaves of a few Cycads are present, but they are not so abundant as they were in the lower stages, and here represent a waning group.

In a survey of this flora as a whole, together with a consideration of the manner of occurrence of certain of its constituent elements, two facts of more than ordinary importance force themselves upon the attention of the investigator: (1) There is an astonishing similarity or striking resemblance between these Cretaceous plants of Europe and America; and (2) the higher Angiosperms appear in identically the same manner in these two widely separated areas, by sudden introduction as if by impulses or waves of migration.

In regard to the first of these propositions, Ward in his excellent paper has shown that the early Cretaceous floræ of

the two continents are very similar. He says,* “We should not, of course, expect the species to be common to any great extent, and the comparison is practically limited to the genera. Looked at from this point of view, we see that the resemblance is indeed close, a great number of the important genera occurring in both floras. There are no less than 46 of these common to the two, though in some cases the author’s individuality is probably alone responsible for slight differences in the terminations in the names.” What is here said of the plant remains from the lower beds is also true of those from the Cenomanian, and in fact the entire Cretaceous flora of the two Hemispheres is strikingly similar.

The second fact of unusual importance is the sudden introduction of the higher Angiosperms in the several strata in which they occur. They first make their appearance in beds below the Cenomanian, but with very few exceptions these species are all strictly representatives of, and belong to, the higher forms. They exhibit few traces of a lower organization, and certainly fall far short of the connecting forms we should expect to find bridging the gap between the Dicotyledons and lower types, if their evolution had taken place in the regions where their remains are now found. It is possible to explain the sudden influx of so extensive, varied, and highly organized a flora as that of the Cenomanian only on the hypothesis of migration, and this migration was, moreover, in all probability due to a climatic change which permitted the species to spread into new localities formerly unfitted for their maintenance. There is no other way in which to account for the remarkable similarity between the floræ of the two Hemispheres, it seems to me, than to assume the existence of a common center of dispersion. All the facts in connection with the distribution of these higher plants offer such a striking analogy to a similar class of facts concerning the higher Mammalia, that I shall have occasion to recur to this subject again.

In the Upper Cretaceous beds of both Europe and America, the remains of a rich flora have been found. I can not better illustrate the character of this flora in America than to quote a few extracts from the work of Professor L. F. Ward, one of the most eminent authorities on paleobotany in America. In describing the types of the Laramie flora, he says,† in speaking of the genus *Ficus*: “Among my Fort Union specimens I have thus far found three species referable to that genus which, if this reference is sustained, and if no others be detected, will show that a climate existed in the Fort Union epoch and at

* Some Analogies in the Lower Cretaceous of Europe and America. Sixteenth Ann. Rept. U. S. Geol. Surv., p. 534, 1895.

† Bull. U. S. Geol. Surv., No. 37, 1887.

the latitude of Glendive [Montana] warm enough and moist enough to permit these chiefly tropical plants to thrive." Again, in speaking of the genus *Cinnamomum*, he says: "An almost exclusively tropical genus embracing about fifty species, confined to the Old World, but ranging on both sides of the equator. Fossil representatives are abundant in the Tertiaries of Europe, especially in the Eocene, but forms are reported as low as the Cenomanian. The four species of the Laramie thus far described argue a warm climate." And again, he says of *Zizyphus*, a genus related to the Buckthorn: "A widely distributed tropical and subtropical genus containing in the present flora about fifty species. It has been hitherto represented by eight Eocene, one Green River and five Laramie species, none of the last being from the Fort Union strata." He describes three species from the Upper Cretaceous of Montana. In like manner he mentions a number of other types of a tropical or subtropical habit from the Laramie, or Upper Cretaceous beds. Lastly, I may mention the presence of Palms of the genus *Sabal*, recently described by Hatcher as an absolutely conclusive piece of evidence in favor of a Floridian climate during this epoch, as far north as Wyoming and Montana.

In the Tertiary, a subtropical climate continued in America as far north as central Wyoming, to near the close of the Eocene. This is proved by abundant remains of Palms in the Green River shale beds, and by the presence of numerous tropical species of Vertebrates and Invertebrates in the Bridger beds. Before the close of the Eocene, however, the temperature in this latitude underwent a change, and by the time the Oligocene is reached a strictly temperate climate had appeared. In Europe, similar changes in the climatic conditions throughout the Tertiary, from an almost, if not quite, tropical temperature through all the intermediate stages to that of a frigid temperature in Glacial time, are to be met with.

Viewed from the standpoint of the fossil plants, therefore, the contention that the Northern Hemisphere has passed through all these phases of climate from torrid to frigid, from early in the Mesozoic to the present, is simply incontestable. The evidence is equally conclusive that the cooling-off process was inaugurated at the Pole and gradually extended to the southward. The assumption, moreover, that the higher Angiosperms originated and were evolved in the more southern latitudes, where they so suddenly appear, is illogical and untenable, not only by reason of the virtual absence of any ancestral forms foreshadowing or leading up to them in the floræ of the older epochs, but by the sudden appearance of the same or closely allied types in identically the same manner and, as far as we

know, at the same time, in localities so widely separated as Europe and America.

If, now, we examine these problems from the standpoint of the distribution of the ancient mammalian faunæ in the Northern Hemisphere, we reach conclusions so strikingly similar, that the two classes of facts taken together constitute such a basis or groundwork of probability, that we may feel reasonably safe in locating the place of origin of both the higher plants and certain mammals, at least, within the polar regions.*

The facts of mammalian distribution in the Northern Hemisphere may be briefly stated as follows: Early in the Mesozoic, there appeared small mammal-like forms, which were widely distributed over both the Northern and Southern Hemispheres. Representatives of these species continued throughout the Cretaceous, and finally disappeared in the early stages of the Tertiary. From these forms the modern Marsupials undoubtedly had their origin. Many of them are classified in the group Multituberculata, which without much doubt finds its nearest living representative in the Duckbill of Australia. It should be here stated that with very few exceptions all these forms are represented by fragments of jaws and teeth. In one instance, however, a fairly complete skull is known (*Tritylodon*) from the Karoo beds of South Africa. The teeth of this species are astonishingly like those of many types in the Northern Hemisphere, and hitherto it has always been classified in this group. Seeley has shown that the organization of the skull presents so many reptilian characters as to cause him to refer it to the Reptilia. If this reference is correct, then in the absence of any facts to the contrary it is highly probable that all the Multituberculates are as much reptile as mammal. Indeed, it is not easy to say at first glance upon which side of the line living Monotremes should be placed. There can be little doubt that, when more fully known, these ancient fossil types will present every conceivable gradation between these two great divisions of the Vertebrata.

One fact in connection with these Mesozoic forms stands out clearly and distinctly, and that is that as far as we are permitted to judge from their fragmentary remains, the progress of their evolution toward any of the higher mammals was very slow indeed. The amount of change registered by their teeth throughout the greater part of the Mesozoic is comparatively insignificant. On this account it is inconceivable that any of the species with which we are at present acquainted should be regarded in the light of ancestors of the higher types, or Eutherian Mammalia.

* Some very noted botanists have held this view of the origin of the Angiosperms within the polar regions; thus Gray, Saporta, and Nathorst were convinced of its truth, and Dawson thought it probable.

The oldest Tertiary strata containing mammalian remains which are at present known are found in the San Juan Basin of New Mexico, and were named by Cope the Puerco. These beds are from five hundred to eight hundred feet in thickness, and apparently lie conformably upon the Laramie, or Upper Cretaceous. Within the lower fifty feet are found the remains of a rich mammalian fauna, thirty-one species in all, composed largely of representatives of the higher, or Eutherian, subclass. Associated with them are five species of Mesozoic types closely related to forms from the older Laramie beds.

In this same region, at a distance of from five to eight hundred feet above the Puerco layer, occurs a second fossil-bearing horizon, which I have called the Torrejon stage. From this bed, forty-four species have been identified, of which five are of the Mesozoic type. The facies of the fauna is very like that of the Puerco, and there are many genera or their derivatives common to the two horizons, but the species are in every case different. Just as the Eutherian mammals in the Puerco bed below were all of sudden introduction, so there were no less than twelve genera which represent entirely new and previously unknown types.

Resting conformably upon the Torrejon comes the Wasatch, the beginning of what we may call the middle division of the Eocene, and here again is a rich mammalian fauna. Deposits of this age are found in the Big Horn, Green River, and Wind River Basins of Wyoming and all have yielded many remains of extinct mammals. Like that of the preceding bed, the fauna of the Wasatch is made up of two elements: One which includes the modified descendants of the older preëxisting types, and another which is entirely new to the region. This latter element in the Wasatch comprises not only new genera and species, but entire new orders. Thus, we meet for the first time with such types as the Rodentia, Artiodactyla, Perissodactyla, besides whole suborders and families included in the Carnivora, Amblypoda, Primates, and Insectivora. Some of these types continue through several subsequent stages and then disappear, while others become the dominant factors in the succeeding development and finally give rise to the modern mammalian fauna. What is here said of the Puerco, Torrejon, and Wasatch, is likewise true of the Wind River, Bridger, and Uinta of the Eocene. New and strange forms constantly appear, of which no vestige nor trace has ever been found in the older beds. Nor is this sudden introduction of new types confined to the Eocene, but is equally true of the Oligocene, Miocene, and Pliocene beds of this country.

The most remarkable circumstance connected with the facts here enumerated is that identically the same thing happened in

the Tertiary deposits of Europe. The succession of these strata is not so complete in Europe as in America, and their record of the appearance and disappearance of mammalian forms is less perfect; however, it is sufficiently complete to give the broad features of mammalian succession. While the Jurassic mammals are well represented, and correspond closely genus for genus with those from the Wyoming beds in America, the Cretaceous forms as well as those corresponding to our Puerco have not been found in Europe. The oldest Tertiary beds in Europe from which mammalian remains have been obtained are those at Cernay in France. According to Osborn,* this fauna bears a close resemblance and corresponds to that of our Torrejon. It is in the succeeding Wasatch or its near equivalents, however, that the most striking similarity occurs. Exposures of beds of this age are found at many localities in Europe, and a fauna almost equal in richness and variety to that of America is known. Just as in America, the sudden introduction of the same entire orders—the true Primates, the Rodentia, Artiodactyla, Perissodactyla, Insectivora, as well as many suborders, families, and genera of the various other groups—takes place without previous warning. The most remarkable fact is the similarity observable in the two faunæ. In many instances, the species belong to the same genera which are common to the two Hemispheres.† In the following succession, the introduction of new types of the same general character as those in America proceeds in the same sudden and unheralded manner.

Now, what is the significance of these facts and from what source or sources were these faunæ derived? In the case of the Puerco, we have the sudden introduction of thirty or more species belonging mostly to a group of mammals hitherto entirely unknown upon the earth. The species of the Mesozoic types may be accounted for by derivation from the preëxisting mammals whose remains are found in the underlying Cretaceous, but as regards the Eutherian element of the fauna, no earlier traces of it have ever been found, and he who would maintain that this new Eutherian element in the Puerco fauna developed from any of the known Cretaceous forms, in the ordinary course of evolution, would be so utterly lacking in a proper sense of morphological proportion as to be a very unsafe guide in such matters. The Laramie or Upper Creta-

* A Review of the Cernaysian Mammalia, Proc. Phila. Acad., 1890.

† The more important of the nearly related or identical genera common to Europe and America in the Wasatch or its near equivalent in Europe, thus far identified, are *Coryphodon*, *Phenacodus*, *Hyracotherium*, *Pantolestes*?, *Paramys* and *Plesiaretomys*, *Heptodon* and *Lophiodon*, *Arctocyon* and *Anacodon*, *Palæonictis*, *Sinopa* and *Proviverra*, *Oxyæna*, *Calamodon*, *Hyopsodus*, and others.

ceous beds are extensively exposed in the same region in which the Puerco fossils are found, and indeed the remains of many characteristic Laramie land Vertebrates occur in the strata immediately underlying those containing the Puerco, but notwithstanding the most careful and extensive search, which I have myself conducted, not a vestige of the Puerco forms has ever been found in these underlying beds. The same is true of the vast stretch of territory along the skirts of the Rocky Mountain divide in which the Laramie is so extensively exposed. Not a tooth, not a scrap nor a fragment of a bone referable to these Puerco Eutherians has ever been found, in spite of the fact that many of the most expert collectors have searched for them assiduously in these localities for many years. It is hardly possible to explain their absence from the Cretaceous on the basis of unfavorable conditions of preservation, for the reason that we have not only the remains of many species of land Vertebrates well and abundantly preserved, but we have Mesozoic mammalian remains as well. The only explanation which seems to me possible is that they were migrants coming into these latitudes for the first time at the beginning of the Puerco.

The same argument applies with equal force to the new elements which were introduced in the Torrejon, Wasatch, Wind River, Bridger, and other epochs. They were simply new-comers representing so many waves or impulses of migration, and the fact that practically the same species were introduced at practically the same time, in the same order, and in the same abrupt manner, in two such widely separated localities as the Eastern and Western Hemispheres, adds overwhelming proof that the two faunæ had a common center of dispersion.

Now, where is it possible to locate such a land area common to the two Hemispheres? Geologists have made out a sufficiently complete history of the continental land masses, as well as of the great ocean basins, to give a tolerably exact idea of the main facts. All are agreed that at no time, at least from the beginning of the Mesozoic to the present, were the broad relations between the oceans and continents, either to the east, west, or south of the localities under consideration, materially different from what they are to-day. There is no evidence whatever of any land connection between the two Hemispheres at or near the Equator at any time in the past, so that the only possible place where this common land area could have existed was in the North.

Let us examine the question again, from the standpoint of the faunal changes which are indicated in the successive deposits of our American Tertiaries. In the Wind River and

Bridger epochs, the general facies of the fauna and flora is that of a tropical or semitropical region, as everyone who has given any attention to the subject is bound to admit. Palms, tropical Invertebrates, Alligators, tropical Turtles, and numerous species of monkeys, give ample proof of the nature of a climate which is to-day so necessary to their existence. In the succeeding Uinta, deposits were made within less than fifty miles to the southward of the typical Bridger localities, and in them we find but few fragments of these tropical or semitropical conditions remaining. The general aspect of the fauna gives evidence of a warm temperate climate, with the appearance of extensive savannas and much open country. In the Oligocene deposits of nearly the same latitude, with the exception of a single specimen of Alligator, no traces of any remains referable to, or characteristic of, even a semitropical climate have been found, notwithstanding the fact that these deposits are among the richest in mammalian remains of any in the world, and have been most thoroughly explored. The monkeys, Palms, tropical Turtles, and Invertebrates had completely disappeared, and there is overwhelming proof to the effect that they migrated to the southward. The European Tertiaries contain the same record, and the evidence that a general southward retreat of both the higher plants and mammals was in progress throughout much of the Cretaceous and the whole of the Tertiary is so complete, conclusive, and incontestable, that it may, in my judgment, be accepted as a fully demonstrated fact.

If, therefore, the sudden introduction of these new elements into the succeeding faunæ and floræ is to be explained upon the basis of migration, we are then in a position to assign a rational cause for its occurrence. We have already seen that the temperature in the region of the Pole was tropical in the early Cretaceous, and that it slowly declined throughout the succeeding epochs until finally a frigid condition was established. The migration of the Puerco fauna we may readily believe to have been caused by the appearance of unfavorable conditions, both climatic and vegetal, which gradually supervened within the limits of its ancient boreal home. In like manner, further modifications of the climate and vegetation in the same region caused the Wasatch exodus, and, like their Puerco predecessors, they had no alternative other than to follow the receding tropical forests to the southward. That some of them remained behind and were gradually modified to fit the new and changing environment, however, there can be also very little question. In this manner and from this cause doubtless arose those types which came finally to dwell in temperate and arctic climates. When changed conditions in the environment

arose, the inhabitants of the region had choice of one of three alternatives; migration, modification to fit the new conditions, or extinction. And I may add that paleontological study concerns itself almost exclusively with deciphering the record of the successes and failures of animal species along these lines.

In the case of the Primates, their structure at the beginning of the Wasatch had been fully adapted to an arboreal existence, as their prehensile extremities so fully demonstrate. Being exclusively dependent on these conditions, they were bound to follow in whatever direction the limits of the tropical forests shifted; and that the recession and gradual retreat of these forests was from within the Arctic Circle in the North to the vicinity of its present confines in the South, during the interval between the Middle Cretaceous and the Glacial epoch, is supported by an overwhelming abundance of evidence. It thus becomes possible, it seems to me, to locate the place of the origin of a large number of the higher Mammalia. Whether a similar series of changes took place at the South Pole, giving rise to its own peculiar types of mammals, is as yet uncertain, but at the same time not improbable. At all events, the Primates belong to the North, and it is within the Arctic Circle that they had their beginning. *

The second inquiry with which we are at present concerned is the kind and character of mammal from which the Primates were probably derived. Unfortunately the evidence necessary for a final solution of this problem is very far from complete. The question of the oldest known Primates has not yet been settled with satisfaction. Certain species from the lower Tertiaries of this country, notably the Puerco and Torrejon beds, have been variously referred to the Primates and Creodonta by investigators who have studied them—Cope, Scott, Osborn, Earle, and Matthew. These animals are known almost exclusively from the teeth, and in a few instances only are any of the

* In this connection I wish to call attention to the admirable work of Hon. G. Hilton Scribner, New York, 1883, "Where did Life Begin?" It is now quite impossible to state by whom this view was first entertained, but the late Professor Asa Gray, in a private letter to Mr. Scribner in 1884, distinctly claimed the credit of having been the author of the migration on north and south lines. Reference to Gray's published writings, however, as well as to those of Saporta, Nathorst, and Dawson, fails to show that any attempt was ever made by any of these eminent investigators to put forward the proofs and formulate the view into a distinct hypothesis of the Polar origin of life. In this Mr. Scribner was clearly the first, and so ably and logically was the Polar Origin theory presented, that Dr. Gray in commenting upon it was led to remark that Mr. Scribner's position was "simply incontestable." In the light of the great mass of evidence now at hand, it is easy to recognize and to appreciate fully the extreme probability of such a view; but when we recall the almost total lack of evidence in its favor at the time Mr. Scribner's book appeared, his work becomes all the more noteworthy, and in my judgment is entitled to a high rank among intellectual performances of a similar kind. This should thus be known as the Scribnerian Theory of the place of the origin of life.

other skeletal parts represented. In comparison with the oldest and most primitive undisputed monkeys, a careful examination of these Puerco and Torrejon forms reveals a wide difference in the organization of the two, and it is much to be doubted whether they really have anything in common with the true Primates. It appears necessary, however, to make an exception to this statement in the case of the genus *Mixodectes* and possibly also of *Olbodotes*. Matthew believes,* from an associated astragalus, that the former of these genera belongs to the Rodentia rather than to the Primates, but its successors in both the Wasatch and the Bridger show very strong Primate affinities; hence, there can be little doubt that they constitute an aberrant side branch of the main Primate axis.

If we thus exclude the *Mixodectes-Microsyops* series, the oldest remains of true and undisputed Primates occur in the Wasatch, and there are excellent reasons for the belief that they were new types of sudden introduction in the region, at the beginning of this epoch. Unfortunately, these Wasatch forms are very imperfectly known, so that it is not until we reach the Bridger that anything like complete skeletons have been obtained. Some, at least, of these Bridger types, while true monkeys, were in practically the same state of evolution as many of the existing lemurs, so that by careful comparison of the two groups we are enabled to eliminate the specialized and advanced features and reach the more fundamental primitive characters which must have belonged to the ancestors of all Primates.

There has been relatively little speculation on the definite and more exact origin of any of the great groups of Eutherian mammals, and apparently less on the Primates than any other. Huxley, in his famous paper "On the Application of the Laws of Evolution to the Arrangement of the Mammalia," expressed the opinion that they arose from a central type of the Insectivora, such as the Erinaceidæ. Nearly twenty years later we find no less an authority than Hubrecht† warmly supporting the same view. In speaking of *Erinaceus* and *Gymnura*, Huxley's exact words are: "in them, even more than other Insectivora, we possess the key to every peculiarity which is met with in the Primates, Carnivora, and the Ungulata." However much I may be disinclined to dissent from the views of so great a master in morphology, we can not disregard the fact that the very large increase in our knowledge of the extinct forms during the past twenty years has materially altered our conceptions of the relations of these groups. It is true that the Insectivora furnish

* Bull. Amer. Mus. Nat. Hist., 1897, p. 265.

† Descent of the Primates, p. 5, 1897.

a type of cerebral circulation which might easily have passed into that of the Anthropeoidea, through the suppression and disappearance of the stapedia branch of the entocarotid; but, as we have already seen, this character is shared by the Rodentia and probably by other groups as well. At the same time it does not furnish a type of cerebral circulation from which that of the lemurs could have been evolved.

The greatest difficulty in the way of deriving the Primates from any form or forms of the Insectivora at present known consists in the total lack of prehensile powers of the manus or pes. Any group which is placed ancestral to the Primates must of necessity be one in which some distinct approach to this condition is made, since its possession is one of the chief requisites of fundamental importance. For this reason, if for no other, the modern types, at least, of the Insectivora, can not be looked upon as the forerunners of, or as more than very distantly related to, the ancestors of the Primates.

With the single exception of *Lophiomys* among the Rodentia, the only other living mammals which exhibit prehensile extremities are found among the Marsupials, and the evidence points very conclusively to the fact that all of them, even those with highly modified limbs for terrestrial progression (as the kangaroos), are descended from ancestors with grasping hands and feet. It is therefore not beyond legitimate supposition to assume the existence of a very considerable group of ancient Metatherians living within the Arctic Circle during Cretaceous time, whose manner of life had already become arboreal. If such a group did exist, it is far more likely that the Primates were derived from it rather than from the Insectivora or any other group now living. Future research and discovery in these regions will alone settle the correctness or incorrectness of this hypothesis, and until such discoveries are made we must be content with the results of speculation.

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XVI, NOVEMBER, 1903.]

SUBORDER CHEIROMYOIDEA.

THE first suborder, or the Cheiromyoidea, is of great interest, inasmuch as it numbers among its representatives the very curious and interesting creature commonly known as the Aye Aye, now living in Madagascar (Plates XI and XII). This species was first brought to the attention of naturalists by the French traveller Sonnerat more than a hundred years ago, and was for a long time looked upon as belonging to the order Rodentia, or the Gnawers, closely allied to the squirrel.

In 1862, Richard Owen received a specimen of the animal, and from a careful study of its anatomy conclusively demonstrated its lemurine affinities. As we have already seen, the character of its incisors and the form and general make-up of its jaws are exceedingly like those of the rodents; but in the complete bony ring surrounding the orbit, as well as in the prehensile extremities and the remainder of its anatomical structure, it bears the unmistakable stamp of its Primate relationship.

The hands are long and slender and the fingers are provided with claws. The third digit of the manus is curiously modified, in that while of the same proportional length as the others it is exceedingly slender. It has, indeed, been aptly compared to a wire with a hook at its end. The animal is nocturnal in its habits, inhabiting the dense forests of Madagascar, where it is said to be rare.

The specimen which was sent to Owen was kept in captivity for some time, and Dr. Sandwith, who obtained the animal, was enabled to learn its curious habits. He wrote as follows: "I observe he is sensitive of cold, and likes to cover himself up in a piece of flannel, although the thermometer is now often 90° in the shade. He is a most interesting little animal, and from close observation I have learned his habits very correctly. On receiving him from Madagascar, I was told that he ate bananas; so of course I fed him on them, but tried him with other fruit. I found he liked dates,—which is a grand discovery, supposing he be sent alive to England. Still I thought that those strong rodent teeth, as large as those of a young Beaver, must have been intended for some other purpose than that of trying to eat his way out of a cage—the only use he seemed to make of them, besides masticating soft fruits. Moreover he had other peculiarities,—*e. g.*, singularly large, naked ears, directed forward, as if for offensive rather than defensive purposes;

then, again, the second finger of the hands is unlike anything but a monster supernumerary member, it being slender and long, half the thickness of the other fingers, and resembling a piece of bent wire. Excepting the head and this finger, he closely resembles a Lemur.

“Now, as he attacked every night the woodwork of his cage, which I was gradually lining with tin, I bethought myself of tying some sticks over the woodwork, so that he might gnaw these instead. I had previously put in some large branches for him to climb upon; but the others were straight sticks to cover over the woodwork of his cage, which *alone* he attacked. It so happened that the thick sticks I now put into his cage were bored in all directions by a large and destructive grub, called here the *Moutouk*. Just at sunset the Aye-aye crept from under his blanket, yawned, stretched, and betook himself to his tree, where his movements are lively and graceful, though by no means so quick as those of a Squirrel. Presently he came to one of the worm-eaten branches, which he began to examine most attentively; and bending forward his ears, and applying his nose close to the bark, he rapidly tapped the surface with the curious second [third] digit, as a Woodpecker taps a tree, though with much less noise, from time to time inserting the end of the slender finger into the worm-holes as a surgeon would a probe. At length he came to a part of the branch which evidently gave out an interesting sound, for he began to tear it with his strong teeth. He rapidly stripped off the bark, cut into the wood, and exposed the nest of a grub, which he daintily picked out of its bed with the slender tapping finger, and conveyed the luscious morsel to his mouth.

“I watched these proceedings with intense interest, and was much struck with the marvellous adaptation of the creature to its habits, shown by his acute hearing, which enables him aptly to distinguish the different tones emitted from the wood by his gentle tapping; his evidently acute sense of smell, aiding him in his search.”

I have quoted thus at length these interesting observations upon the grub-eating habits of the Aye Aye, for the reason that there can be no doubt, apparently, that they are directly responsible for the rodent-like character of the incisors, as well as for the tendency to degeneration and reduction of the molars and the curious modification of the third finger of the hand which is made to fulfil the functions of a probe, pleximeter, and scoop. We shall presently see in what way these modifications throw light upon some of the extinct American forms of this same group.

The chief diagnostic features of the suborder have already been given, and to these should be added the lack of bony

union of the two rami of the lower jaw, as in the Rodentia. It is probable that this condition is in some way correlated with the enlargement of the incisors and their final growth from persistent pulps, as seen in the most advanced species. Of the extinct American forms, I recognize two groups, which, on account of the wide differences between them in point of structure, I classify in two distinct families. The structure of one of these groups is imperfectly known, and it is impossible to state with certainty whether or not they are Primates. Osborn has recently proposed* to arrange them as a primitive suborder of the Rodentia, Proglires, but there are so many serious objections to such a view that I choose to regard them as Primates allied to *Cheiromys*. My reasons for such a course will be given after the species have been described.

The suborder as thus constituted includes three families, defined as follows :

Incisors reduced to a single pair above and below, enlarged, faced with enamel, and growing from persistent pulps, rodent-like ; premolars reduced to one above and absent below ; molars quadritubercular above and below, and rodent-like in pattern, with tendency to degeneration. *Cheiromyidæ*.

One pair of incisors above and below, enlarged, recurved, transversely compressed, and slightly twisted ; crowns sheathed with enamel, not growing from persistent pulps, and altogether unlike those of rodents ; cheek teeth in lower jaw reduced to two small styliform rudiments inserted immediately behind the large incisors ; upper cheek teeth unknown. *Metacheiromyidæ*.

One to three pairs of incisors in the lower jaw, with central pair enlarged, having distinct roots, and with crowns sheathed in enamel ; premolars never less than two in lower jaw ; molars tritubercular above, with fourth cusp rudimentary ; anterior cusp of trigon present in lower molars ; fourth premolar becoming molariform above and below. *Microsyopsidæ*.

Family Metacheiromyidæ fam. nov.

Metacheiromys Marshi gen. et sp. nov.

The remains upon which this family and genus are founded consist of a single specimen of a fragmentary skeleton, which includes the two upper incisors, with a portion of the premaxillary attached ; portions of the back and base of the skull, including an otic bulla ; one mandibular ramus, with the entire tooth-border preserved ; the bodies of nearly all the cervicals ; a few dorsals and caudals ; some ribs ; the glenoid cavity of the scapula ; the proximal and distal ends of a humerus ; the proximal and distal ends of an ulna ; the distal end of a radius ; a portion of the pelvis, and the proximal and distal ends of a tibia.

* American Eocene Primates, etc., Bull. Amer. Mus. Nat. Hist., June 28, 1902.

The superior incisors, figure 105, more nearly resemble the upper canines of *Hapalemur griseus* than any other teeth with which I have been able to compare them. They are, however, less pointed, somewhat thicker in front, and have a decided twist. The office of this torsion was doubtless to bring into apposition flat-wise the points of the two teeth implanted by diverging roots. Both the crowns and the roots are considerably compressed from side to side, the crown terminating behind in a sharp cutting edge. In cross section, therefore, the tooth gives an elliptical outline, pointed behind. There is a worn surface upon the front face of the crown, showing the point where it most frequently impinged upon the lower incisor. The crown is completely invested with enamel, and the tooth was implanted by a distinct root and was therefore of

FIGURE 105. — Superior incisor of *Metacheiromys Marshi* Wortman; side view; natural size. (Type.)

limited growth. The remaining cranial fragments furnish little information of the general skull structure further than that there was a well-ossified tympanic bulla more or less filled with cancellous tissue.

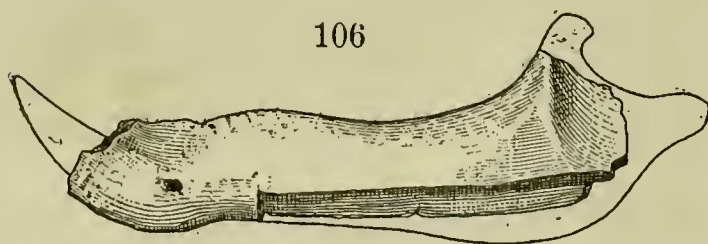


FIGURE 106. — Lower jaw of *Metacheiromys Marshi* Wortman; side view. (Type.)

FIGURE 107. — The same jaw; viewed from above.

Both figures are one and one-half times natural size.

107



Although not complete, the lower jaw, figures 106 and 107, exhibits some remarkable characters. Posteriorly the lower edge is broken away, as well as the coronoid, condyloid, and angular regions. The front third, however, is entire, and in this part the ramus displays an unusual lack of depth, but is of normal transverse thickness. This latter dimension is consider-

ably augmented in the region of the implantation of the single enlarged incisor. The crown of this tooth is not preserved, being broken away at the level of the alveolus. The root is suboval in cross section, with a rounded angular part internal. Projecting the contour of the broken part of the jaw from that which is preserved, the horizontal ramus is seen to be rather shallow and slender. There was a well-developed masseteric fossa, the anterior portion of which is shown in the specimen. That which may be regarded as the most extraordinary feature of the jaw is the practical absence of cheek teeth. The dentinal border is preserved entire and in this are to be seen two shallow sockets, the first of which is situated immediately posterior to the enlarged incisor. After a short interval behind, a second similar alveolus occurs, and it is perfectly evident that these served for the implantation of two single-rooted styliform teeth, which were apparently caducous. The remainder of the tooth border was entirely edentulous. The mandibular symphysis is not rugose, and there is no trace of any tendency to coössification of the two rami.

The characters of the bodies of the cervical vertebræ are of an indifferent nature, and furnish little or no information of the affinities of the species. They are rather broad and depressed, and are without inferior keels, as in the rodents and certain lemurs, notably *Nycticebus*. The caudal vertebræ denote that there was a long tail. The ribs, as indicated by a few heads, are likewise of the usual pattern and wholly uncharacteristic.

The glenoid cavity of the scapula has a form usually seen in the living lemurs, perhaps more resembling that of *Propithecus* than any of the other existing species. It will, however, answer quite as well for that of a squirrel. The humerus, figure 108, is more characteristic, and it is in this bone that the Primate affinities begin to manifest themselves. The head is globular, somewhat pointed behind, and overhangs the shaft but slightly. The greater tuberosity rises to the level of the head, and is of considerable fore and aft extent. It equals slightly more than one-half the anteroposterior diameter of the articular portion. The lesser tuberosity is also prominent and separated from the greater tuber-

108

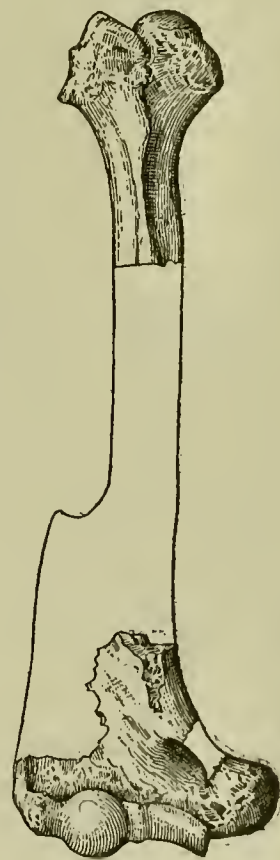


FIGURE 108.—Right humerus of *Metacheiromys Marshi* Wortman; front view; natural size. (Type.)

osity by a distinct bicipital groove. The deltoid crest is moderate, but the extent to which it descends upon the shaft can not be determined on account of the imperfect condition of the bone. Upon the whole, its proximal end presents a very strong likeness to that of *Cheiromys* and *Propithecus* among the Primates, and differs from that of the rodents. The distal end is noteworthy for its great proportional breadth. The internal condyle is prominent, as in all early mammals. There is an entepicondylar foramen and an unusually broad supinator ridge. On account of the incompleteness of the latter, it is impossible to state whether it terminated abruptly above, as in *Cheiromys*, or sank gradually away into the shaft, as in *Propithecus* and the other lemurs. The distal articular extremity presents the usual divisions into trochlear and capitellar portions. A characteristic feature of this part of the Primate humerus is a ridge descending from the shaft in front, to become continuous with the external raised edge of the ulnar articular surface. No trace of this ridge is found in the humerus of the Rodentia, but in the fossil it is present, although not so strong as in existing lemurs and monkeys. The trochlear portion for articulation with the ulna is well rounded and terminates behind in a moderately deep olecranon depression. The capitellar portion is unusually globular and displays upon its outer side a distinct groove which extends somewhat more than halfway around the articular extremity.

Among living forms, the only case in which this groove is so well developed is in *Propithecus*. *Cheiromys*, *Galago*, and *Cheirogaleus* exhibit distinct traces of it, but it is confined to the upper outer edge of the capitellum. In *Propithecus* it is associated with a characteristic shape of the articular head of the radius, which consists of a central depression surrounded by a more or less flat ringlike area around the edge. The head of the radius is not preserved in the fossil, but the similarity in the structure of the corresponding humeral articulation leaves little doubt that its form was like that of *Propithecus*. The distal end of the humerus is thus seen to be like that of the lemurs and entirely different from that of *Paramys* and *Sciurus*, with which I have compared it.

The olecranon of the ulna is unusually long, and in this respect differs from all the modern lemurs, as well as from *Sciurus*. It is deeply grooved upon its outer side and presents an extensive, flattened, subcutaneous area upon its under side. In the first of these characters it resembles the ulna of *Propithecus*, and in the second that of *Cheiromys*. The similarity to these two genera also extends to the distal ends of both the ulna and radius.

The tibia, figure 109, is the most characteristic part of the skeleton preserved, and in the absence of the feet this bone, especially in its distal end, may be said to be one of the most distinctive of the entire Primate skeleton. The chief characteristics of the tibia in the lemurs and monkeys may be briefly stated as follows: The proximal surface is divided into two subequal articular facets, which are separated by a relatively high, pointed tibial spine. The long, straight shaft is much compressed from side to side and marked at the lower part of its upper third in front by a roughened tubercle for the attachment of the *semitendinosus*, one of the chief inner hamstring muscles. The distal extremity is relatively narrow transversely and limited internally by a large pointed malleolus. The articular surface which it offers to the astragalus is slightly concave from before backward, but in a transverse direction is almost plane and slopes outward toward the fibula. This arrangement is associated with a highly characteristic form of the astragalus, which in turn is indicative of a prehensile pes. Among the Rodentia, on the other hand, the tibia and astragalus are equally characteristic and distinctive of another type of foot. In the fossil under consideration, the tibia has every mark and feature of the Primate so unmistakably stamped upon it that I have no hesitancy in referring the species to this order, in a position not far removed from *Cheiromys*.

Discussion.—We have already seen that in *Cheiromys* we have an undisputed Primate, in which the incisors have undergone modification exactly similar to that of the Rodentia. We have further seen that the presence of these teeth in this animal is associated not only with a peculiar modification of the third finger of the hand, but with a grub-eating habit and a tendency to degeneration of the molars and premolars. Now in the extinct creature before us, we have, if the evidence derived from its osteology can be trusted, an equally unmistakable Primate undergoing the same modification of the incisors, and

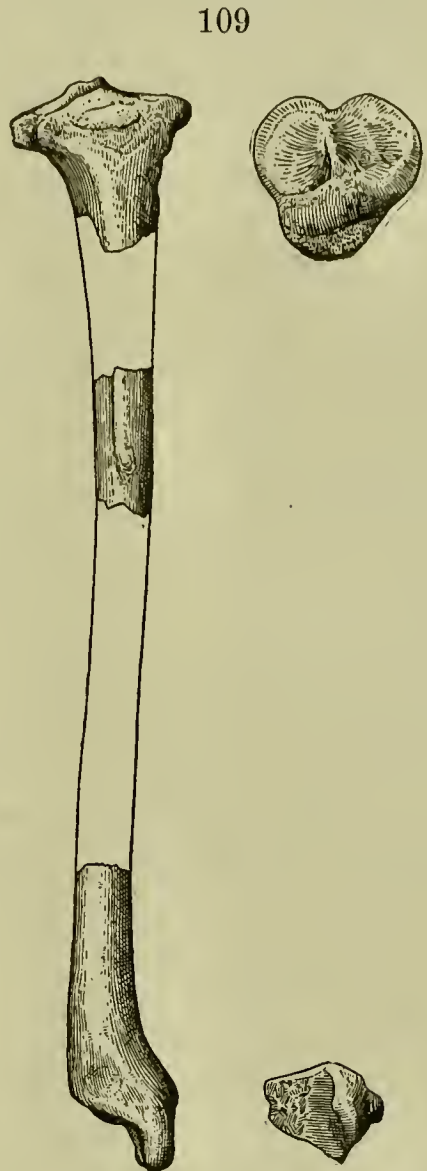


FIGURE 109.—Right tibia of *Metacheiromys Marshi* Wortman; front and end views; natural size. (Type.)

in which the cheek teeth had almost completely disappeared. We have no information of the structure of the hand, but whether or not any of the fingers were modified in a manner corresponding to that of the Aye Aye, the practical loss of the molars and premolars can be accounted for on no other supposition than that the nature of the food upon which the animal subsisted was so soft as to require no crushing power on the part of the grinders. From what we know of the habits of the Aye Aye, the inference is both logical and natural that this food was also soft larvæ, which the animal was doubtless accustomed to seek in a similar way. From the comparative slenderness and weakness of the lower jaws, we may even further suggest that the animal captured these grubs in soft or decayed wood.

If the facts of structure have been correctly interpreted and our hypothesis in regard to the habits is well founded, what shall we say of the relationship between *Metacheiromys* and *Cheiromys*? Is it possible to suppose that these modifications, so profound and unique among the Primates, have originated twice in the same group entirely independently of each other? *Metacheiromys* can not be placed directly in the ancestral line of *Cheiromys* for the reason that by the loss of the grinders it had, in the Eocene, already reached a more advanced stage of evolution than the living genus. But to deny that the two were descended from a common ancestral stock would, it seems to me, involve such a tremendous assumption as to lay a heavy burden upon our powers of belief. Such assumption becomes all the more onerous in the complete absence of any evidence in its support. If one had no proofs upon which to base an opinion respecting the community of origin and distribution from a common center other than that afforded by these two animals, so widely separated in space and yet so closely connected in structure, he could still feel amply assured of the security of his foundations. This evidence of the relationship between the Madagascar and Wyoming species, therefore, adds but another link in the chain of proof already set forth, that both forms were migrants from a common boreal home.

Family Microsyopsidæ.

Microsyops Leidy.

The next family of this group to be considered is the Microsyopsidæ. The type genus *Microsyops* was separated and described by Leidy in April, 1872.* In June, 1871, Marsh had previously described a species, *Hyopsodus gracilis*,† which

* Proc. Acad. Nat. Sci. Phila., 1872, p. 20 (published April 16).

† This Journal, vol. ii, 1871, p. 42.

Leidy, at the time he proposed the genus *Microsyops*, thought to be identical with the specimens he had in hand, and adopted Marsh's specific name *gracilis*. Marsh, however, in the same paper in which he described *Hyopsodus gracilis*, had proposed another species, *Limnotherium elegans*. From an examination of Marsh's types, Leidy afterward concluded that it was to *L. elegans* that his specimens were to be referred, and that *Hyopsodus gracilis* was a different species. His exact words are: * "The specific name of *M. gracilis* was originally given under the impression that the remains referred by Professor Marsh to *Hyopsodus gracilis* pertained to the same [species of] animal. A specimen exhibited to the writer by Professor Marsh would indicate that *M. gracilis* is the same as the animal named by him *Limnotherium elegans*. As *Microsyops* is generically distinct from *Limnotherium* as characterized from the typical species, *L. tyrannus*, the specific name of the former would be *Microsyops elegans*."

A careful examination of the types confirms Leidy's conclusions as given above, and establishes the further important fact that *Hyopsodus gracilis* of Marsh is not only distinct specifically, but represents an apparently undescribed genus of the Microsyopsidæ. The oldest members of this group come from the second stage of the Lower Eocene, or Torrejon beds, of New Mexico. The first species of this group found was described by Cope as *Mixodectes*.† Quite recently Osborn has added a second genus *Olbodotes*.‡ The chief characters of *Mixodectes*, which is known almost exclusively from lower jaws, are the following: There are eight teeth in the jaw, of which three are molars, three are premolars, one is a canine, and one an incisor; the last premolar is much simpler than the molars in structure; the two incisors, representing the central pair according to Osborn, are moderately enlarged.

Olbodotes has a full incisor dentition in the lower jaw, with a tendency to enlargement of the central pair. The premolars are reduced to two and the fourth premolar is simpler than in *Mixodectes*. It is therefore the most primitive species of this group thus far known, if correctly referred to this series.

From the succeeding Wasatch, Cope has described another genus under the name of *Cynodontomys*. This species, while very much like the Torrejon *Mixodectes*, differs from it in having lost either the canine or the second premolar and in the greater enlargement of the incisors.

In the Wind River, we have the first appearance of the genus *Microsyops*, which differs from *Cynodontomys* in the

* Extinct Vertebrate Fauna of the West, 1873, p. '84.

† Amer. Philos. Soc., 1882-1883, p. 550.

‡ American Eocene Primates, etc., Bull. Amer. Mus. Nat. Hist., 1902, p. 206.

more complex and perfectly molariform character of the fourth premolar. In the Bridger, from which the type of the family was derived, there are at least four well-marked species now known. The characters of the genus, as understood almost exclusively from the dentition, are as follows: There is but a single pair of incisors in the lower jaw and presumably a like number in the upper jaw; the enamel is not limited to the anterior face of the tooth, as in the Rodentia, but completely invests the crown, and the teeth are not of continuous growth; a small canine and two premolars are present, or no canine and three premolars, according to the way in which we interpret the first small tooth behind the enlarged incisor to be a premolar or canine; except, perhaps, in one species, the fourth premolar above and below is completely molariform; the superior molars are tritubercular in structure, with a faint beginning of a fourth cusp and a slightly developed mesostyle, which becomes stronger in the later species; the two rami of the lower jaws are not coössified.

I know of no remains of other parts of the skeleton that with certainty can be referred to any species of the genus. I have seen, however, some skeletal fragments which I strongly suspect belong to a species of this genus, but I lack the evidence to make the necessary connections.

Microsyops elegans Marsh.

Limnotherium elegans Marsh, this Journal, January, 1871, p. 12; *Microsyops gracilis* (in part) Leidy, Proc. Acad. Nat. Sci. Phila., 1872, p. 20; *Mesacodon speciosus* Marsh, this Journal, September, 1872, p. 205; *Palæacodon verus* Leidy, Proc. Acad. Nat. Sci. Phila., 1872, p. 20; *Microsyops elegans* Cope, Tertiary Vertebrata, 1883, p. 217; *Microsyops gracilis* Osborn, American Eocene Primates, Bull. Amer. Mus. Nat. Hist., 1902, p. 210.

Description of the Type.—The type of this genus and species consists of a fragment of a left mandibular ramus bearing the first and second molars, together with the fourth premolar, and the roots of the last molar. The anterior and posterior parts of the jaw are not preserved, so that it is impossible to determine the full dentition. The molar crowns may be described as consisting of an anterior, tricuspidate, elevated portion, usually termed the trigon, and a posterior, wider, less elevated part, or heel. The three cusps of the trigon are conical, and are placed in the form of a more or less perfect equilateral triangle, with the apex directed forward. Of these, the anterior is much the smallest of the three, the two posterior cusps being subequal in size and standing nearly opposite each other. The heel is considerably wider than the anterior, or trigonal, part of the crown and bears three distinct cusps enclosing a basin. Of these, one is external, one internal, and one posterior. The external cusp is the largest and

has a V-shaped pattern. One arm of the V extends forward and inward to join the base of the trigon and the other inward and backward to the posterior cusp. The internal cusp is relatively small and conical, and situated directly opposite the large external one. In front of this, between it and the internal cusp of the trigon, is a deep notch through which the valley opens internally. The posterior cusp of the heel is small and indistinct; it is situated upon the posterior rim of the central valley, more to the inner than to the outer side; it is connected with the outer V-shaped cusp by a low ridge, and is separated from the inner cusp by a notch. The crown of the fourth premolar is nearly like that of the true molars, the only noticeable difference in its structure being the absence of the anterior cusp of the trigon, together with the smaller size and more posterior position of the interior trigonal cusp. The chief characteristics of these teeth are seen in the broad heel as compared with the trigon, as well as the slight elevation and distinctness of the cusps of the latter.

Description of the Type of Mesacodon speciosus.—The specimen upon which this genus and species were founded

110

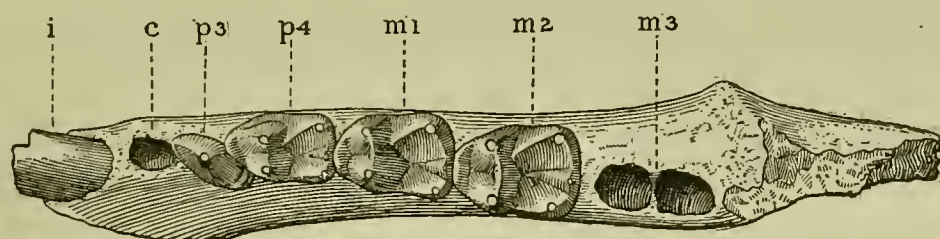


FIGURE 110.—Lower jaw of *Microsyops elegans* Marsh (type of *Mesacodon speciosus* Marsh); viewed from above; two and one-half times natural size.

consists of a well-preserved lower jaw, figure 110, of the right side, lacking the condylar, coronoid, and angular portions. The last molar is missing, as well as the canine or second premolar and the crown of the large incisor. After careful comparison with *Microsyops elegans*, I can not discover any difference between the two. The teeth are very nearly of the same size and, as far as ascertainable, the crowns of the molars and premolars are constituted in exactly the same way. I do not hesitate, therefore, to refer them to the same genus and species.

The additional information furnished by this specimen permits an accurate determination of the entire dentition of the lower jaw. The enlarged incisor is implanted by a distinct root and was not, therefore, of persistent growth; its position is procumbent, being directed much forward and a little upward. Most of the crown is broken away, but enough remains to show that the enamel was not limited to the anterior face of the tooth, as in *Cheiromys* and the Rodentia, but invested

it posteriorly as well as in front. The canine or second premolar follows without diastema, and judging from the size of its alveolus was relatively large. An indistinct ridge upon the inner side of the socket indicates that the root was grooved in this situation, a fact which is against its interpretation as a canine and in favor of its being a premolar. The third premolar had not been fully erupted at the time of death, and is only partly protruded from the jaw; it is implanted by two roots somewhat diagonally to the long axis of the ramus and has a pointed crown, with a small, though distinct, heel. The fourth premolar is identical in structure with that of the type of *M. elegans* already described, as are also the molars. The last molar is not preserved in either specimen. The ramus is deepest in front at the posterior border of the symphysis, narrowing considerably behind. The tooth line does not pass behind the coronoid to such an extent as in *Cheiromys* and the Rodentia. The anterior border of the masseteric fossa is prominent and, as in both *Cheiromys* and the Rodentia, toward its upper posterior portion forms the root of the coronoid, which therefore has a position much external to the tooth line. The opening of the inferior dental canal lies considerably below the level of the tooth crowns—a character in which it agrees with *Cheiromys* and differs from both the modern squirrels and *Paramys*. It may be further noted that the symphysis is roughened, but not coössified with the opposite ramus.

Description of other Material.—There are in the Marsh collection six other specimens of more or less complete lower jaws, which I refer to this species. Among these specimens there are several examples of a last molar. This tooth very closely resembles the other molars in structure, differing only in the elongation of the heel by reason of the greater size and prominence of its posterior cusps. In no case do any of the upper teeth accompany these lower jaws, but in another species to be described later, there are upper and lower teeth in association, so that the form of the upper molars is known with certainty. In my own collection there is a well-preserved upper jaw of a small form of *Microsyops*, bearing all the molars and the last premolar, which accord so well in size with what the upper teeth of *M. elegans* should be, that I have no hesitancy in attributing it to that species. I obtained this proportional size by measurement of the teeth of many living species of lemurs, as well as of those of the one known *Microsyops* above referred to.

There should be also mentioned here, the species described by Leidy under the name *Palæacodon verus*, from a superior molar. According to Leidy's figure, this tooth, figure 111, is identical with the upper teeth which I refer to *Microsyops elegans*, and it therefore becomes a synonym of that species—

a conclusion which has been already reached by Osborn. The more important features of the upper teeth of this species may be stated as follows: There are three molars, of which the first and second are subequal, with the third smaller; the crown has three main cusps and a faint indication of the fourth; the two outer cusps are more or less crescentic in structure; there is a small though well-marked mesostyle; both intermediates are present in the first and second molars, but the posterior is absent in the last; the fourth premolar is molariform, but lacks any trace of the posterior intermediate. I give herewith a reconstruction in outline of the dentition, figure 112, as derived from several specimens.



FIGURE 111.—Upper molar of *Microsyops elegans* Marsh (type of *Palæacodon verus* Leidy); crown view; twice natural size. (After Leidy.)

FIGURE 112.—Upper and lower jaws of *Microsyops elegans* Marsh; side view; natural size; composed from several individuals.

The measurements of the type of *Microsyops elegans* are as follows:

From base of posterior root of last molar to anterior extremity of crown of fourth premolar	16.0 ^{mm}
From base of posterior root of last molar to anterior extremity of crown of first molar	11.0
Length of fourth premolar and first and second molars	11.0
Length of first and second molars	7.5

The measurements of the type of *Mesacodon speciosus* are:

Length from posterior root of last molar to base of incisor	20.0 ^{mm}
From base of incisor to posterior extremity of fourth premolar	7.5
Depth of jaw at posterior border of symphysis	8.0
Depth of jaw at last molar	7.0

Measurements of the last lower molar and upper teeth of other specimens:

Length of upper molars	10.5 ^{mm}
Length of upper molars and fourth premolar	14.5
Length of last lower molar	5.0
Length of second and third lower molars	8.5

The type specimen was found by Professor Marsh, at Grizzly Buttes, Bridger Basin, Wyoming. The type of *Mesacodon speciosus* was also found by Professor Marsh at the same place. Other specimens are recorded from this locality; also from Dry Creek, and from Millersville. The single specimen which I obtained is from the same horizon as that in which the type was found.

Microsyops gracilis Leidy.

Microsyops gracilis Leidy, Proc. Acad. Nat. Sci. Phila., April 16, 1872, p. 20; *Bathrodon typus* Marsh, this Journal, August, 1872, p. 19, Separata; *Microsyops typus* Osborn, Bull. Amer. Mus. Nat. Hist., 1902, p. 212.

As already noted, Leidy, in his final description of *M. gracilis*, believed it to be the same as *M. elegans*. This is undoubtedly true of the first specimen mentioned, but a second lower jaw was associated with the latter, with the expression of some doubt as to its specific identity. There are in the Marsh collection four specimens, exclusive of the type of *Bathrodon typus*, figure 113, consisting of the upper and lower jaws of a form which agrees in every way with the figures and descriptions given by Leidy of his second specimen. These are supplemented by three more examples of upper teeth obtained by myself in the type locality last summer. The additional material enables me to determine that this series of specimens is not only larger than the typical *M. elegans*, but

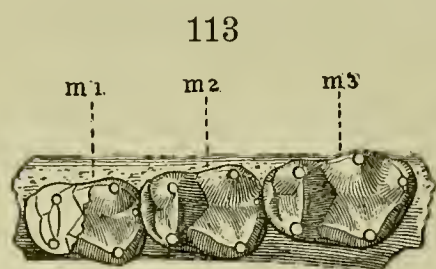


FIGURE 113.—Lower jaw of *Microsyops gracilis* Leidy (type of *Bathrodon typus* Marsh); viewed from above; two and one-half times natural size.

FIGURE 114.—Upper jaw of *Microsyops gracilis* Leidy; crown view; twice natural size.

presents other constant differences which I think impossible to account for on the basis of differences in age or sex. In no case are the upper teeth, figure 114, associated with those of the lower jaw, but as in the preceding species, the size and character of the two correspond so closely that there can be virtually no doubt of their relations. The more important distinctive characters are the following: The teeth are slightly larger than those of *M. elegans*, and the jaw is appreciably heavier and deeper; the last upper molar has a distinct mesostyle and a posterior intermediate cusp, both of which are absent in the same tooth of *M. elegans*; the fourth superior premolar has a mesostyle and the posterior intermediate dis-

tinged; the external cusps of the superior molars are apparently less flattened and crescentic than those of *M. elegans*.

In one specimen of an upper jaw, the second and third premolars are preserved, although the tooth which I take to be the second is not in place. The third is implanted by three roots, two of which are external and one internal. The crown is composed of a single large external and a smaller internal, or lingual, cusp. The second is a two-rooted tooth, much smaller than the preceding; its crown is a simple, transversely flattened cone, with a slight indication of a heel, and is very much like the corresponding tooth in many of the modern lemurs. No other parts of the skeleton are known, but I here call attention to an unassociated calcaneum, figure 115, which

is not only Primate, apparently, but is about the right size for this or the preceding species and may possibly pertain to one of them. The Primate characters of the bone are seen in the short and incurved tuber, as well as in the arrangement of the facets, which are much like those in *Lemur catta*. The chief peculiarity, however, is in the elongation of the part below the astragalar facet, recalling at once the elongated calcaneum of some of the modern Madagascar species. I mention this matter for the reason that there is no other known Primate in the

Bridger to which, as regards size, it could pertain. If this supposition is sustained, these animals are certainly Primates.

The measurements of the type of *Bathrodon typus* are as follows:

Length of second and third molars. 8.25^{mm}

Measurements of other specimens:

From base of last molar to base of incisor	22.00 ^{mm}
Length of first and second molars	9.00
Length of fourth premolar and first and second molars	12.50
Depth of jaw at posterior border of symphysis	9.00
Depth of jaw at anterior border of third molar	10.00
Length of upper molars	11.00
Length of upper molars and fourth premolar	15.00
Length of third and fourth premolars and molars	18.00

The type of *Bathrodon typus* was found by Mr. F. Meade, Jr., at Grizzly Buttes; other specimens were obtained at Church Buttes and Millersville. I secured specimens on Cottonwood Creek and at Church Buttes. The calcaneum was found on Dry Creek.

115



FIGURE 115. — Calcaneum of *Microsyops* (?); dorsal view; twice natural size. *af*, astragalar facet; *st*, sustentaculum tali.

Microsyops annectens Marsh.

Bathrodon annectens Marsh, this Journal, vol. iv, August, 1872, p. 19, Separata; *Microsyops annectens* Osborn, Bull. Amer. Mus. Nat. Hist., June, 1902, p. 213.

The type of this species, figure 116, consists of a fragment of a lower jaw of the left side, bearing the last molar. The only character by means of which it can be distinguished from the two preceding species, at least as far as the type is concerned, is that of size. This distinction, however, is so pronounced that the validity of the species can not be questioned.

116

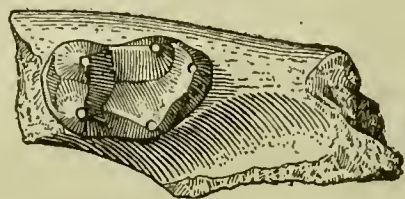


FIGURE 116. — Last lower molar of *Microsyops annectens* Marsh (type of *Bathrodon annectens* Marsh); crown view; two and one-half times natural size.

The crown of the last molar has identically the same structure as that of *M. elegans* and of *M. gracilis*. The trigon is slightly elevated above the heel and the anterior cusp is not very distinct. The heel displays its characteristic breadth, with the large external lunate cusp and the smaller external and posterior cusps. The posterior cusp is not situated at the center of the posterior border, but very much to the inner side, in a position almost behind the internal—an arrangement which gives an imperfect quadrilateral outline to the heel. This is highly characteristic of the genus *Microsyops*, and insures its recognition at sight.

In the present collection, there are four other specimens represented by lower jaws alone, which give the lower dentition in its entirety. The form, proportions, and relations of the other teeth are very like those in the two species already described.

The measurements of the type are as follows :

Length of last molar	5.8 ^{mm}
Depth of the jaw at anterior margin of third molar ...	11.0

Measurements of other specimens :

Length of molar series	16.0 ^{mm}
Length of second and third molars	10.0
Length of molars and premolars to base of incisors ...	30.0

The type specimen was found near Henry's Fork, by Mr. F. Meade, Jr., of the Yale party, in September, 1871. Additional specimens from the same locality were obtained by Mr. Harger and others.

Microsyops Schlosseri sp. nov.

This species is founded upon a fragment of a left mandibular ramus, figure 117, bearing the second and third molars, together with two fragments of the upper jaw containing the first and second molars in one, and the second molar in the other. There is also an anterior portion of a jaw, bearing a part of the incisor and the premolars much worn, which I likewise refer to this form.

The chief difference between this species and *M. annectens* is one of size. It exceeds *M. annectens* to about the extent that the latter exceeds *M. gracilis*. Another feature of importance is seen in the wrinkled surface of the enamel, especially in the valley of the heel, where it is quite rugose. The anterior cusp of the trigon is small, though distinct, in the crown of the first molar, but consists of little more than a thickened cingulum in the second. The internal cusp of the trigon is broken, but apparently had about the same degree of elevation as is usual in the other species. The jaw is notably heavier than that of *M. annectens*.

Associated with the type lower jaw is a second upper molar which seems to be too much worn to belong to the same individual. The specimen, however, was collected by Professor Marsh himself, and knowing his great care in such matters, there must have been in the manner of their occurrence very good reason for putting the two together. A second isolated fragment of an upper jaw includes the first and second molars. The chief characters of these teeth are as follows: The outer cusps are moderately flattened externally; the mesostyle is distinct, though small; the intermediates are as in the other species; the postero-internal cusp is represented by little more than a cingulum in the second, but is more distinct in the first; the enamel is rugose.

The following are the chief measurements of the type and of the upper molars referred to this species:

Length of second and third lower molars.....	12.0 mm
Length of last lower molar	6.5
Depth of jaw at anterior border of third molar.....	10.5
Antero-posterior diameter of first and second upper molars	10.5
Transverse diameter of second upper molar	6.0

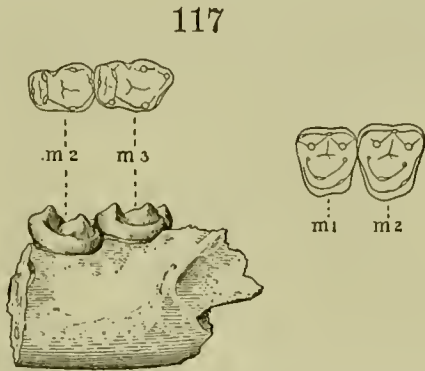


FIGURE 117.—Upper and lower molars of *Microsyops Schlosseri* Wortman; side and crown views; one and one-half times natural size. (Type.)

The type specimen was found by Professor Marsh, at Henry's Fork of Green River, August 9, 1873. The other specimens were obtained at the same locality.

In addition to the species herein described, there are probably at least two others indicated by fragmentary specimens. One of these consists of an upper molar tooth of a small species about equal in size to *M. elegans*. It comes from the upper horizon of Henry's Fork, and differs from the upper teeth which I have attributed to *M. elegans* in the absence of the mesostyle, absence of intermediates, and the greater prominence of the postero-internal cusp. It apparently belongs to *Microsyops*, but I refrain from proposing a specific name for so fragmentary a specimen.

In like manner, there is a fragment of an upper jaw containing two molars, from the lower horizon. The structure of these molars differs from all other species of *Microsyops* from the Bridger beds in the more distinctly conical shape of the external cusps, as well as in the prominence of the intermediates. I suspect that the form may be the same as one of the Wind River species in which the upper teeth are entirely unknown.

Smilodectes gen. nov.

This genus is founded upon the specimen originally described by Professor Marsh under the name of *Hyopsodus gracilis*. Osborn in his synonymy refers it to *Sarcolemur*, but the structure of the teeth distinctly forbids its reference to either of these genera. In certain respects the dentition, as far as known, resembles that of *Microsyops* more than that of any other genus, but in others it exhibits distinct relationship to that of *Notharctus* and *Limnotherium*. The number of teeth in the lower jaw is eight, as against seven in *Microsyops*, of which the most anterior is an enlarged incisor. Just as in *Microsyops*, the succeeding tooth may be rated either as a canine or an incisor; if a canine, there are then three premolars and if a premolar, there are four. The fourth premolar is not molariform. The single enlarged incisor distinguishes the genus from *Notharctus* and *Limnotherium*, and the more complex fourth premolar from *Mixodectes*.

Smilodectes gracilis Marsh.

Hyopsodus gracilis Marsh, this Journal, July, 1871, p. 42.

The type of this species and genus consists of the anterior part of a left mandibular ramus, figure 118, containing the fourth premolar, first molar, and a portion of the third pre-

molar. Parts of the alveoli for all the remaining teeth in front are also recognizable, so that the number of the teeth can be accurately determined. With this I associate three other specimens, in two of which the last molar is well preserved.

The jaw has about the same depth as that of the larger species of *Microsyops*, which it otherwise resembles in its general form. The symphysis is deep and rugose, projecting somewhat below the level of the lower border of the ramus, but exhibits no traces of coösfication. The alveolus of the enlarged incisor lies close to the symphysis, and unlike that of *Microsyops* indicates an almost vertical position for this tooth.

Immediately behind the incisive alveolus is a medium-sized socket for the first premolar or canine. Behind this comes a two-rooted tooth, with the larger of the roots posterior. The third premolar is likewise two-rooted. A portion of the crown denotes that there was a slight indication of a heel. The rest of the crown is broken away. The fourth premolar is in about the same stage of evolution as that of *Limnotherium* or *Notharctus*. The internal cusp, however, is smaller, but the heel is broader and provided with two cusps instead of one. The first molar also closely resembles that of *Limnotherium tyrannus*, lacking the great transverse breadth of the posterior part of the crown seen in *Microsyops*. The arrangement of the cusps is very similar to that seen in *Limnotherium*.

I also place in this species three specimens in which the last lower molar is preserved, but which do not show the number of teeth. The association may be therefore incorrect. In one specimen, part of an upper molar is preserved which exhibits a structure like that of *Microsyops*, and not like that of *Limnotherium*. The last lower molar, on the other hand, resembles the same tooth in *Limnotherium* more than that of *Microsyops*, from all of which, in connection with the characters of the type, I conclude that the specimens must be referred to the species under consideration.

The last molar differs from that of *Microsyops* in the central position of the posterior cusps. In *Microsyops*, as we have already seen, this cusp stands almost directly behind the internal one. In this respect the tooth resembles the last molar of *Limnotherium*, but the cusp is not so large and is more distinct from the posterior rim of the heel. Again this molar differs from that of *Limnotherium* in having a distinct internal

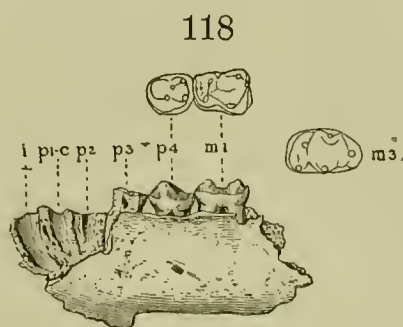


FIGURE 118. — Anterior portion of lower jaw (type of *Hyopsodus gracilis* Marsh) and last lower molar of *Smilodectes gracilis* Marsh; side view of jaw, and crown views of teeth; one and one-half times natural size.

cusps of the heel, as in *Microsyops*. Associated with one of the specimens containing the last lower molar is a portion of an upper molar. Enough is preserved to show that there were three main cusps, together with a rudimentary fourth, very much as in *Microsyops*.

The type specimen was found by Professor Marsh, at Grizzly Buttes, Bridger Basin, on September 5, 1870; other specimens were obtained at the same locality.

The Relationship of the Microsyopsidæ.

There is as yet no absolutely conclusive evidence by means of which the position of this group can be determined with certainty. The species had always been considered, without good reason, to belong to the Primates, until Matthew, from an associated astragalus of *Mixodectes pungens*, put forth the view that these forms are rodents. Osborn following Matthew, placed them in a primitive suborder of the Rodentia, which he called Proglires. He says:* “*Relationship to the Rodentia* is now found to be indicated by: (1) progressive elongation of median incisor; (2) disappearance of lateral incisor; (3) reduction of canines; (4) disappearance of the anterior premolars and reduction of third premolar; (5) transformation of fourth premolar into molar forms, thus foreshadowing a homodont molar-premolar series; (6) width and extension of talonid (as in Eocene *Paramys*); (7) rodent form of astragalus. *Against the Rodent relationship* are: (1) Persistence of the canine; (2) absence of diastema; (3) absence of any evidence (except the levelling of the premolars) of adaptation for antero-posterior or orthal motion of the jaw.”

If the astragalus which Matthew associates with the lower jaw of *Mixodectes* really pertains to the same animal, there is then strong presumptive proof that this species, at least, is not a Primate. From long personal experience in collecting in the Torrejon beds, however, I have found that only too frequently the fossils are washed out of their original matrix and badly mixed. Without a full knowledge of the circumstances under which these particular specimens occurred, and in the absence of reasonably conclusive evidence which would tend to preclude the possibility of a mixture, I should not feel inclined to attach any very great weight to this association. At all events, I should wish some stronger evidence upon which to rest so important a generalization. As for Osborn's alleged additional evidence of relationship to the Rodentia, attention may be called to the fact that he seems to have overlooked *Cheiromys* and left it out of account entirely. With the

* American Eocene Primates, etc., Bull. Amer. Mus. Nat. Hist., 1902, p. 204.

exception of the character of the astragalus, which, as we have just seen, is open to question, all the characters cited, save one—the molariform fourth premolar—are evidence of relationship with, and apply equally to *Cheiromys* as well as to the Rodentia. The molariform fourth premolar is not an especially rodent character. It occurs among the Lemuroidea in *Hapalemur griseus*, *Otogale Monteiri*, *Galago Alleni*, and *Hemigalago Demidoffi*. In like manner, the evidence against rodent relationship, as given by Osborn, can be quite as well considered to be evidence against relationship to *Cheiromys*, for Owen has long since conclusively demonstrated that this species is a Primate, with a highly modified rodent-like dentition. Altogether, I fail to see wherein Osborn has given any reasons, beyond those already well known, for regarding the Microsyopsidæ as members of the Rodentia. On the contrary, to my mind, there is fairly conclusive proof that these animals are not rodents. I shall now proceed to a statement of this evidence.

In Part I of the present series of papers (p. 96, Separata), I have presented my views at some length upon the theory of "Cusp Migration," as originally propounded by Osborn.* I have likewise dissented from the use of the terminology of the mammalian molar cusps proposed by him, on the ground that their homologies were incorrectly determined and the names applied inappropriate and misleading. I have further expressed the opinion that, as far as any nomenclature is applicable to these cusps, which would convey any information of their homological relationship, that proposed by Scott is preferable because based upon ascertained and undisputed facts in the history of the premolar series. By far the most important principle embodied in Scott's determination of the order of appearance and homological position of the cusps of the premolars, although never expressed nor stated by him, is that by means of which we are provided with the key to a proper interpretation of the molar cusps and the determination of their history. All theoretical considerations, as well as all the evidence obtainable, point with such directness and definite precision to the conclusion that the molars and molariform premolars have passed through identically the same changes and have been subjected to precisely the same influences, that it may be accepted as one of the basic and fundamental truths of dental morphology. Credence in any other view would be equivalent to believing that the corresponding teeth on the opposite sides of the mouth have had different histories. This principle or law has not as yet been ocularly demonstrated, for the reason that no Eutherian mammals older than those from

* Jour. Acad. Nat. Sci. Phila., 1886, p. 242.

the Tertiary are known. In the earliest Eocene, the molars, with a few notable exceptions, had already assumed such a degree of complexity as practically to obliterate all traces of the order of appearance and manner of development of the cusps. When, however, the ancestors of the Puerco fauna are found, and the more primitive stages of their tooth development obtained, I look forward with the utmost confidence to the production of all the evidence necessary to a complete and final demonstration of the truth of this hypothesis.

While this principle, enunciated by Scott, may be made to include any given group of mammals, and the history of their molar cusps thus determined, yet at the same time I feel well assured that no general law can be framed nor can any terminology be devised which will be applicable to all the Mammalia, unless it is confined strictly to the position of the cusps, without any reference whatever to their homologies. The reason for this difficulty is, that different groups of mammals have adopted different plans for increasing the complexity of their molars. In many divisions, the order of appearance and position of the cusps, as outlined by Scott, undoubtedly obtains; but in others, as I shall presently show, it has been different.

Taking as a starting point a transversely flattened conical crown, a complicating premolar of the inferior series, in a large number of groups of the Mammalia, passes through the following stages: (1) The posterior edge or slope of the crown elongates and develops a second or posterior root; (2) this slope of the crown becomes thickened transversely, and flattened from before backward, so as to present a triangular area with the apex at the summit; (3) this area looks upward and backward, and is bounded by a descending ridge on each side; (4) a thickened ledge is formed at its base, foreshadowing the heel; (5) on the *inner* descending ridge, bordering the posterior triangular area, appears a new cusp, small at first, which is *posterior and internal to the main cusp*; (6) concomitantly, the heel broadens and its posterior edges grow up in such a way as to form a basin; (7) at the same time a cusp may or may not be developed, at the anterior slope of the crown; (8) the heel develops two cusps, one of which is external and one internal in position.

Thus, it will be seen that all the elements necessary to the formation either of the quadritubercular or of the so-called tuberculo-sectorial crown are present, and further growth of the new elements is all that is required to effect a complete molariform transformation. That the evolution and development of certain premolars has taken place in this manner, is supported by a great abundance of evidence from many well-known phyla whose history has been determined with consid-

erable exactness. In connection with teeth having this developmental history, one important point to remember is, that the antero-internal cusp, or the one which originates upon the inner ridge of the posterior triangular area, is always slightly posterior to the antero-external or main cusp. And it is also of the *utmost importance* to recall that the apex of the original single-pointed premolar corresponds to, and is homologous with, the antero-external cusp. This has been determined as true of the Ungulata, Carnivora, Insectivora, Primates, and probably of other orders.

In the case of the Rodentia, however, it is different. If a perfectly unworn, lower fourth premolar of a member of the Sciurormorph division is examined, figure 119, it will be seen that the new cusp, instead of originating upon the internal, is an outgrowth of the *external*, descending ridge bordering the posterior triangular area. It thus happens that the cusp which corresponds to, and is homologous with, the apex of the original single-pointed premolar *is the antero-internal and not the antero-external cusp, as in the orders just referred to.*

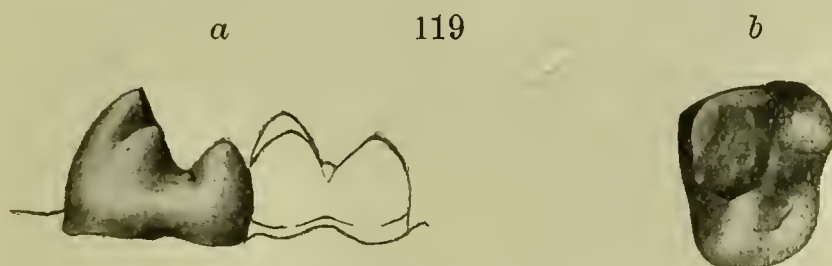


FIGURE 119.—Fourth lower premolar of a species of *Paramys*; outside (a) and crown (b) views; three times natural size.

Further proof of this is found in the fact that the antero-internal cusp has a position in advance of that of the antero-external, which should be the case if the new element had arisen upon the external instead of upon the internal ridge. The ancestral type of the Sciurormorphs is represented by the genus *Paramys* of the Eocene, figure 119, and in this group the manner of origin of the premolar cusps is clearly shown. Distinct traces of this succession are still visible in the squirrels and spermophiles of the present day. The genus *Mysops* of the Bridger beds (*Eomys* of the European Eocene), while closely allied to *Paramys*, without much doubt represents the beginning of the Myomorph division of the Rodentia, and it is interesting to note that this same plan of origin of the cusps of the lower premolars is true of this group as well. No sufficiently primitive stages of the teeth of either the Histricomorphs or the Lagomorphs have to my knowledge as yet been found, which would enable one to say with absolute certainty whether or not the complication of their teeth has

followed this plan or some other,* but I think there can be little doubt that it is a rule of very general application and a fundamental character of the entire order.

From this it follows that no names can be given to these cusps unless we wish merely to indicate their position. Professor Osborn, in reply to my strictures upon his cusp nomenclature, says that "although wrong the names should still stand." His terminology was proposed to supersede the old names then in vogue, which attempted nothing more than to indicate position. This proposal was elaborately made, and its adoption has been strenuously insisted upon, on the ground that the homologies of the cusps had been determined and that Osborn's system thus expressed something more than the mere fact of position. The names themselves carry with them the significance of this alleged homology, which, according to the oft-repeated and many-times-published statements of its author, constitutes one of its chief merits. In view of the facts above set forth, however, I am more firmly than ever of the opinion, that all such attempts are foredoomed to failure, and I believe they should be abandoned as utterly useless and confusing; that of Professor Osborn, being doubly erroneous, is therefore the most open to objection in this regard.

The *Microsyopsidæ*, as we have already seen, follow the Primates in the plan of addition of the cusps to the premolars and presumably to the molars also, which, to my mind, effectually disproves Osborn's suggestion that they are members of the Rodentia. If further evidence is required, we have only to refer to the great dissimilarity in the structure of the molars in the two groups. In no living rodent does the molar pattern approach that of *Microsyops*, except, perhaps, in the squirrels and their extinct forerunner, the Eocene *Paramys*, but even here the differences can be readily detected. Among the Lemuroidea, on the other hand, the great similarity in the constitution of the molar crowns to those of the *Microsyopsidæ* is apparent at a glance. Add to this, the completely transitional molar pattern afforded by *Smilodectes*, together with the strong evidence that the contemporary *Metacheiromys* was a Primate, and the proof of their relationship is all but demonstrated.

* *Sciuravus* Marsh, of the Bridger, which in many respects is closely related to *Paramys*, furnishes the beginning of a modification leading directly into such types of molar crown as those seen in *Steneofiber*, *Palæocastor*, and *Castor*. In like manner, *Mysops* and *Sciuravus* afford the stem types from which both the Histicomorphs and Myomorphs were in all probability derived. This subject will be more fully treated in a subsequent part of the present work.



EXPLANATION OF PLATE XI.
Cheiromys madagascariensis, the Aye Aye. (After Owen.)





EXPLANATION OF PLATE XII.

Cheiromys madagascariensis, the Aye Aye ; showing the slender third digit of the hand
(After Owen.)



[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XVII, JANUARY, 1904.]

SUBORDER ANTHROPOIDEA.

IN a previous part of the present work, I have given the characters by which this suborder is distinguished from the Cheiromyoidea and the Lemuroidea. I have likewise proposed and defined three divisions of the Anthropoidea, of which *Tarsius* and its allies constitute the first (Paleopithecini), the living marmosets the second (Arctopithecini), and the remaining higher Primates the third (Neopithecini). Of the twelve or more species of the Anthropoidea now known to occur in the Bridger, the organization of at least three can be determined with some degree of satisfaction from the material now at hand. This information is not limited to any one part, but includes nearly every portion of the skeletal structure. It is reasonably clear, therefore, that these three species are primitive members of the Neopithecine division of the Anthropoidea. In like manner, the skull of the Wasatch species—the so-called *Anaptomorphus homunculus*—is sufficiently complete and well preserved to show that it is a very near relative of the living East Indian *Tarsius*, and hence a member of the Paleopithecini. The remaining nine or more species from the Bridger are represented mostly by teeth alone, and it is therefore not an easy matter to decide correctly to which of the three groups these forms belong.

As regards the Arctopithecini, or the living marmosets, our knowledge is confined almost exclusively to the existing species. It has been already noted that some of their characters are unique among the Primates. Whether the lack of opposability of the pollex and hallux is to be looked upon as a degeneration from a former more perfect condition of prehensility of the extremities, or whether it represents a stage in the process of acquirement of the opposability of these digits, can not now be determined. It is worthy of note, however, that the internal cuneiform and the proximal end of the articulating metapodial resemble the corresponding parts of the lemurs and monkeys much more than those of any other animal; and, notwithstanding the lack of opposability, this likeness would be sufficiently close to indicate their ordinal position did we know the marmosets from their skeletons alone. There are at the same time some peculiarities in the make-up of these bones, which would lead the cautious anatomist to hesitate in pronouncing upon the opposability of the hallux, especially if

he were to take into consideration the clawed condition of all the digits. The habits of the marmosets, while as strictly and completely arboreal as in any of the Primates, resemble those of the squirrels more than those of the monkeys proper. According to Bates, who had excellent opportunities for observing them in their native forests, the Negro Tamarin (*Midas ursulus*) confines itself mostly to the larger branches, and is frequently seen passing up the perpendicular trunks, clinging to the bark with its claws in a manner not dissimilar to that of the squirrels. This method of climbing is doubtless true of all the marmosets, and the lack of opposability of the hallux and pollex is correlated with the possession of sharp compressed claws instead of flattened nails.

The tritubercular upper molars furnish another character of considerable importance in determining the relationship of the marmosets to the other groups. No Primate of the Eocene is known to possess fully quadritubercular molars. Some of the Adapidæ have a rudimental fourth cusp, but the crown can not be said to be as fully quadritubercular as that of the higher modern apes. By far the greater number of the species have simple tritubercular upper molars, and with the exception of the marmosets and *Tarsius* all the modern representatives of the Anthropoidea have four fully developed cusps. It follows, therefore, that these two groups are survivals from this early condition of the tritubercular stage of development of the molars, and that their detachment from the main axis could not have taken place later than the Eocene. The loss of the last molar in the marmosets, while unusual for a Primate, has clearly taken place since that time, as in the Eocene all the known species have three fully developed molars. There is still another feature of importance exhibited by certain of the marmosets, which is worthy of notice. Forsyth Major found that, out of nineteen skulls of *Hapale* examined, in six the lachrymal extends beyond the orbit to such an extent as to join the nasal and exclude contact between the maxillary and frontal.* This is also true of two skulls of this genus in the Peabody Museum, and I am satisfied that this more primitive condition of the lachrymal is by no means of infrequent occurrence among these species of marmosets. These features are associated with a characteristic lack of depth of the lower jaw, a subglobular form of the condyles, and small size of the lower canines, which do not exceed the incisors, all of which constitute so many steps in the approximation to certain of the Paleopithecine apes of the Eocene. Upon the whole, I am fully persuaded that the ancestors of the marmosets must be sought for among the members of this latter group, and that

* Proc. Zool. Soc. London, Feb. 19, 1901, p. 146.

they had not departed very widely from the parent stock at the close of the Eocene. One of the earliest recognizable characters in the dentition by which they can be distinguished will undoubtedly be found in the reduction in the last molar. It is doubtful, moreover, whether in the history of this phylum the hallux and pollex have ever been opposable.

SECTION PALEOPITHECINI.

Tarsius spectrum is the only living member of this group, and on this account its skeletal organization has an unusual interest for the paleontologist. In many particulars it still retains the generalized features which characterized its Eocene ancestors, while in others it has added some structural modifications, due doubtless to adaptation to slightly different modes of life. These characters relate to the loss of one pair of lower incisors, the development of a bony partition between the orbital and temporal fossæ, the reduction of the fibula and its coössification with the tibia, the grooving and broadening of the astragalus, and lastly the great elongation of the calcaneum and navicular. These modifications of the hind limbs are evidently in relation with, and the result of, saltatory habits, since *Tarsius* in common with all the lemurs having elongate tarsals is a powerful leaper.

The arboreal habits of the Primates have prevented in large measure the development of any great cursorial powers on the part of any of the species, but the habit of leaping from branch to branch has proved of manifest advantage to some of them in the capture of their prey, for in a number of the living species of lemurs this habit is almost as pronounced and highly developed as in certain groups of the Rodentia, the kangaroos, and others. According to Mr. Bartlett, late Superintendent of the London Zoological Gardens, Garnett's Galago is an especially active leaper. In speaking of this species, in a letter to Duncan quoted in Cassell's Natural History, Vol. I, p. 215, he says: "The other night I took an opportunity of letting one of these interesting creatures—Garnett's Galago—have his liberty in my room, and I assure you I was well repaid by his performance. Judge my utter astonishment to see him on the floor, jumping about *upright* like a Kangaroo, only with much greater speed and intelligence. The little one sprung from the ground on to the legs of tables, arms of chairs, and indeed on to any piece of furniture in the room; in fact, he was more like a sprite than the best pantomimist I ever saw. What surprised me most was his entire want of fear of Dogs and Cats. These he boldly met and jumped on at once, and in the most playful manner hugged and tumbled about with them, rolling over

and over, hanging on their tails, licking them on the head and face. I must add, however, that now and again he gave them a sharp bite, and then bounded off, full of fun at the noise they made in consequence of the sly nip he had inflicted. This active trickery he never appeared to tire of; and I was myself so pleased on witnessing the droll antics of the creature that the night passed and it was near daybreak before I put a stop to his frolics by catching and consigning him to his cage. In bounding about on the level ground, his jumps, on the hind-legs only, are very astonishing, at least several feet at a spring, and with a rapidity that requires the utmost attention to follow. From the back of a chair he sprang, with the greatest ease, on to the table, four feet distance."

The other species of *Galago*, as well as those of the Madagascar *Cheirogaleus*, also exhibit much activity, and have the power of leaping great distances in proportion to their generally diminutive size. Duncan says of the Senegal *Galago* (*Galago senegalensis*):* "It pursues Beetles, Sphinges, and Moths with great ardour, even while they are on the wing, making prodigious bounds at them, and often leaping right upwards to seize them. Should it by chance miss its object and accidentally fall from the branch to the ground, it re-ascends with the rapidity of flight to renew the hunt."

Tarsius is also a powerful leaper for so small an animal, and although not larger than a small common squirrel is said to make prodigious springs, both in the branches of the trees and on the ground, in pursuit of its prey.

Among many other groups of Mammalia, the leaping habit is by no means uncommon, and as a result important structural changes in the limbs are to be met with. In all such cases, however, if any modification of the hind limbs takes place in response to this mode of progression, it is almost without exception the metatarsus alone that is affected. Thus, among those forms of Rodentia in which the saltatory habit is most highly developed, as the Jerboas, the Cape Jumping Hare, and others, the metatarsals are greatly elongated and modified. The same is true of the characteristic leapers among the marsupials, as exemplified by the kangaroos and their allies. The development of this habit in certain of the Primates, however, has affected, not the metatarsals, but the tarsals, and the elongation is found in the calcaneum and navicular. This arrangement is unique among the Mammalia, and occurs in no other group of the Vertebrata except the Batrachia, notably the tree-frogs, as was long ago pointed out by Huxley.†

The cause for this modification of the tarsal bones to the

* Loc. cit., p. 238.

† The Anatomy of Vertebrated Animals, 1872, p. 389.

exclusion of the metatarsals is not certain, but it is in all probability in some way associated with the retention of the opposable hallux in the development of the elongated pes. It is of interest to note just here that the fourth digit of all those Primates with elongated tarsals is very perceptibly the longest and strongest of the series, more so, in fact, than in those species in which the tarsals are not elongated. It is all but certain that if this modification were to continue in an exclusively terrestrial habitat long enough to cause the opposable hallux to disappear, the fourth digit would become enlarged and modified, as in the kangaroos and their allies. The chief differences would, of course, be in the elements elongated. The shifting of the axis to the outside and the specialization of the fourth digit are the strongest possible proof that the foot of the kangaroo has been derived from an ancestral type in which the hallux was fully opposable, and hence indicating an arboreal habitat for its possessor. *Tarsius* is the most highly modified of all the Primates with respect to the elongation of the tarsals, as is shown by the reduction in size and the coössification of the fibula with the tibia, as well as in the grooving and broadening of the astragalus. It is in this species that the preponderance in the length and strength of the fourth digit over its fellows is greatest.

Of the known representatives of Eocene Primates in North America, there are no less than six or seven genera, including at least twelve species, which are more or less closely related to *Tarsius*. The skull is known in two of these species only, the remainder being represented by teeth and jaws exclusively. On account of the incompleteness of many of these remains it is quite impossible to determine whether they are members of the Paleopithecini or Neopithecini. It will require a knowledge of the relations of the lachrymal, as well as of the structure of the limbs, before these points can be finally determined. That they do not belong in the Lemuroidea is shown by the characters of the lower incisors and canines, which are known in all the species with the exception of one or two. As a mere matter of convenience in grouping, I arrange a number of these species temporarily in the Paleopithecini. In so doing, however, I wish to state distinctly that there are very good reasons for regarding some of them, at least, as true monkeys, directly ancestral to certain of the living South American forms. This will be further discussed under the descriptions of the species.

The divisions of these species of Primates into family and subfamily groups is in the present state of our knowledge attended with much difficulty. In one series including the genera *Omomys*, *Hemiacodon*, and probably *Euryacodon* also,

there are nine teeth in the lower jaw, which with little doubt are to be interpreted as two incisors, one canine, three premolars, and three molars. In another series which includes *Anaptomorphus*, *Washakius*, *Necrolemur*, and presumably *Microchærus*, there are only eight teeth in the lower jaw, as in *Tarsius*. In this latter genus, the missing tooth is known to be an incisor, and it is almost equally certain that in *Anaptomorphus* it is a premolar. In *Necrolemur*, although perfect lower jaws bearing the full inferior dentition are known, it is quite impossible correctly to assign the teeth in the front of the jaw to their proper categories. In the case of *Washakius*, if the total number of teeth is correctly determined to be eight in each lower jaw, then it is reasonably certain that the missing tooth is an incisor, as in *Tarsius*. Just what significance is to be attached to those differences can not now be properly estimated, but if among the living Lemuroidea the presence or absence of one tooth does not indicate more than a subfamily distinction, I fail to see why such a character should be regarded as of greater importance among the extinct forms. It has been customary with some authors to associate *Microchærus* and *Necrolemur* in a separate family, and remove them from the American species, on account of the complexity and more advanced character of their teeth. It has, in fact, been insisted upon by Leche* that they belong to the Lemuroidea. If, however, the carotid circulation is like that of *Tarsius*, they, with the American forms, probably belong in the Paleopithecini; and the complexity of their teeth will no more entitle them to distinct family rank than that of the Indrisinæ would cause them to be classified as a separate family of the Lemuroidea. The differences in tooth structure between *Necrolemur* and *Hemiacodon* are not as great as they are between *Propithecus* and *Lemur*.† I therefore provisionally arrange these extinct forms in a single family Anaptomorphidæ, with at least two well-marked subfamily divisions. There can be no doubt apparently that *Tarsius*, by reason of the modification of its hind limbs and because of other modernized features, should be placed in a distinct family.

* Untersuchungen ueber das Zahnsystem lebender und fossiler Halbaffen. Festschrift für Carl Gegenbaur, Leipzig, 1896.

† That *Necrolemur* and *Microchærus* exhibit some striking resemblances to the Indrisinæ among the Lemuroidea, however, is certain, and it may well be that in these forms we have the ancestors of this group of lemurs and a true transition from the more or less upright position of the lower incisors to that of the procumbent implantation.

Family Anaptomorphidæ.

The family is divisible into two subfamilies, as follows :

Nine teeth in the lower jaw.

Omomyinæ.

Eight teeth in the lower jaw.

Anaptomorphinæ.

Subfamily Omomyinæ.

The genera of this subfamily are distinguished by the following characters :

Lower molars having three cusps on trigon, the anterior cusp of the last molar not being as distinct as that of the others ; heel of last molar with three cusps ; first and second molars narrow in front, with wider heel ; last molar slightly smaller than first and second, with heel very little wider than trigon ; fourth lower premolar with small internal cusp and an indistinct heel ; third lower premolar without internal cusp or heel, but having a pointed crown whose summit rises above the crowns of the other teeth ; canine larger than incisors or second premolar ; neither first nor second incisor enlarged ; superior molars tritubercular, with rounded external angles, and but moderately extended transversely ; intermediates faint or absent ; a rudimental postero-internal cusp present on first, less distinct on second, and absent on third molar ; first and second molars subequal, third slightly smaller.

Omomys.

Lower molars having three cusps on trigon, the anterior of the third being least distinct ; heel of last molar with three cusps ; first and second molars narrow in front, with broader heel ; last molar longer but narrower than first and second, with heel very little wider than trigon ; fourth inferior premolar with strong internal cusp and distinct heel ; third premolar with rudimental internal cusp and heel ; summit of crown not high and pointed as in *Omomys* ; second premolar, canine, and external incisor small and of equal size ; first incisor enlarged ; superior molars tritubercular, with squarish outline externally, and with intermediates very distinct ; a small distinct postero-internal cusp on first and second molars, but absent on third ; a strong cingulum continued around inside of crown, and developing an additional cusp at the antero-external angle of the crown.

Hemicodon.

Lower molars having three cusps on trigon, the anterior cusp of the last molar being absent ; heel of last molar without distinct internal cusp ; first and second molars without much disparity in width between trigon and heel ; last molar narrow and reduced ; premolars, incisors, and canines unknown ; superior molars tritubercular, with rounded external angles ; intermediates small, but distinct ; a postero-internal cusp on crown of second molar ; cingulum continued around in front, developing a small cusp internal to the main internal cusp ; last molar considerably reduced.

Euryacodon.

Omomys Carteri Leidy.

Omomys Carteri Leidy, Proc. Acad. Nat. Sci. Phila., April, 1869, and Extinct Fauna of Dakota and Nebraska, 1869, p. 408, pl. xxix, figs. 13, 14; *Hemiacodon nanus* Marsh, this Journal, August 13, 1872, p. 213; *Palæacodon vagus* Marsh, this Journal, September, 1872, p. 224.

The type of this genus and species consists of a right mandibular ramus containing the third and fourth premolars and the first and second molars, together with the alveoli of all the remaining teeth of one side of the jaw. The specimen was found by the late Dr. J. Van A. Carter, near Grizzly Buttes, in the Bridger Basin, and is preserved in the collection of the Philadelphia Academy. A comparison of the type of *Hemiacodon nanus* with Leidy's very excellent figure, as well as with Osborn's outline drawing from a photograph of the type of *Omomys Carteri*, renders it perfectly clear that the two are not only generically but specifically identical. Another type which in all probability belongs to this species is *Palæacodon vagus*. This latter consists of three superior molars of the right side in perfect condition. In no specimen of the fifty or more individuals of *Omomys Carteri* contained in the Marsh collection are there upper and lower teeth in association, and I base my opinion that these superior molars of *Palæacodon vagus* are the upper teeth of *O. Carteri* upon the following considerations: In a closely allied species of the same genus, *O. pucillus*, in my own collection, there are upper and lower teeth which were found together in such a way as to render it reasonably certain that they belong to the same individual; there is a decided resemblance between the structure of the corresponding teeth of the two forms; in size the teeth of *P. vagus* correspond almost exactly with what the upper teeth of *O. Carteri* should be, as indicated by the relative measurements of the upper and lower teeth of *Hemiacodon gracilis*, *Tarsius spectrum*, and *Anaptomorphus homunculus*, in all of which the upper teeth are known; they do not agree in size with the lower teeth of any other known species of Bridger Primate. I therefore conclude that the type of *Palæacodon vagus* refers to the upper teeth of *Omomys Carteri*.

Description of the Type of Hemiacodon nanus.

The specimen upon which Professor Marsh established this species consists of a fragment of a right mandibular ramus, figure 120, containing the fourth premolar and all three molars in perfect preservation. The crown of the fourth premolar when seen from above has a somewhat squarish outline, slightly wider behind than in front, and is composed of a main central pointed cusp which arises a little above the level of the cusps of the molars. Upon the outside this cusp is convex, and internally

somewhat concave. A sharp ridge descends from the apex of the main cusp in front, curving gently inward to terminate at the base of the crown in a small, though distinct, anterior cusp developed from the cingulum. Posteriorly the principal cusp is flattened in such a manner as to present a triangular face looking upward and backward. Upon the descending ridge forming the inner border of this triangular area is a small, but distinct, internal cusp, which stands internal and posterior to the main cusp. The posterior face of the crown descends steeply to an indistinct ledge at the base, which is the rudiment of the heel. There are no additional cusps developed, however, in this situation, and the heel may be said to be practically rudimental or absent. It is a matter of importance to note the relations of the cusps, since they serve to explain the structure of the succeeding molars. There is a slight cingulum surrounding the base of the crown in front.

The first and second molars are of nearly equal size, and like those of so many other primitive Primates their crowns are composed of an anterior, narrow, triangular portion bearing three cusps—the trigon, and a broader posterior basin-shaped moiety—the heel. The trigon of the first molar is most distinct, and the three subequal cusps are arranged in the form of an equilateral triangle. If the external cusp is taken

as the apex, the base coincides almost exactly with the tooth line. It results from this arrangement that the internal cusp is situated posterior and internal to the external cusp, which corresponds to, and is strictly homologous with, the main cusp of the premolar in advance. The anterior cusp of the trigon is well developed, of a distinctly conical form, and projects slightly forward in advance of the crown. The heel broadens rapidly, and is composed of a large V-shaped external, and a smaller, more or less conical, internal cusp, inclosing a depression or valley. This valley is completed behind by two ridges passing inward and backward from the two cusps of the heel. At the angular point where these two arms meet, a slight swelling of the enamel occurs, which may be spoken of as an additional cusp.

The second molar differs but little from the first, the only noticeable variation being that the anterior cusp of the trigon is considerably smaller, less conical, and occupies a more posterior position. The external and internal cusps of the trigon are likewise more nearly opposite each other, or transverse to the long axis of the jaw.

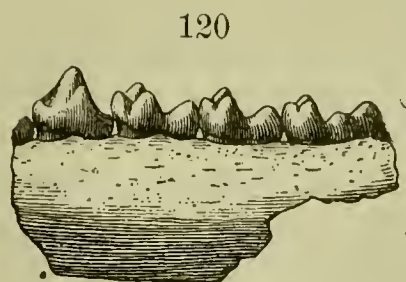


FIGURE 120.—Fragment of a right lower jaw of *Omomys Carteri* Leidy (type of *Hemiacodon nanus* Marsh); inside view; two and one-half times natural size.

The third molar differs from the two in advance of it in showing a still further reduction of the anterior cusp of the trigon, which can hardly be said to be distinct, as well as the presence of a well-developed third cusp and a more elongated

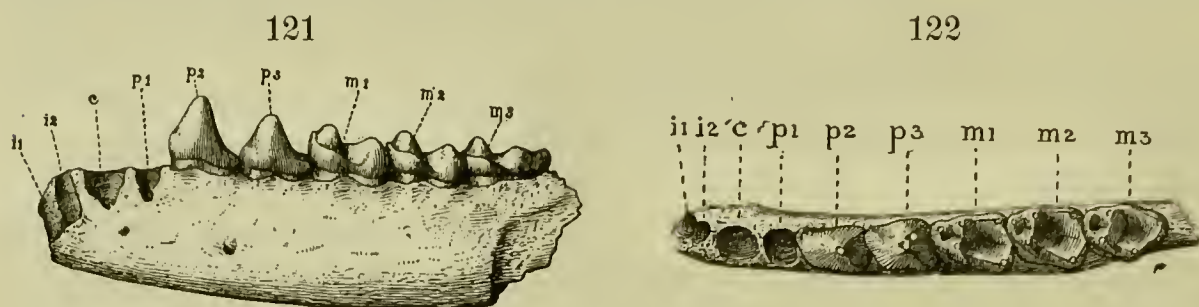


FIGURE 121.—Left lower jaw of *Omomys Carteri* Leidy; showing the alveoli for front teeth; external view; two and one-half times natural size; drawn from two specimens.

FIGURE 122.—Crown view of the preceding figure; two and one-half times natural size.

heel. It is also noticeably narrower, and in many respects distinctly smaller, than the anterior molars. The heel has a large submedian cusp, which stands a little nearer to the inner than to the outer side of the crown.

From the great number of additional specimens of this species in the collection, it is possible to learn the exact dental formula of the lower jaw, which is shown in the accompany-

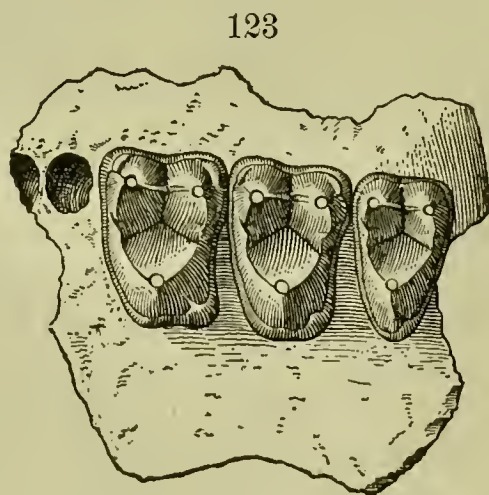


FIGURE 123.—Crown view of three superior molars of *Omomys Carteri* Leidy (type of *Palaeacodon vagus* Marsh); four times natural size.

The cingular cuspule internal to the main antero-internal cusp of the first molar is worn away in the specimen, and has not been indicated by the artist with sufficient distinctness. The external cusps are more flattened externally than is shown in the drawing.

ing cuts, figures 121 and 122. There is no specimen in which the crowns of the incisors, canines, or first (second) premolar are preserved, but that of the second (third) is shown in several examples. Its chief characters are as follows:

There is a single high pointed cusp, which rises considerably above the remaining teeth; there is no internal nor ante-

rior cusp; the heel is little developed, and there is a faint indication of a cingulum in front.

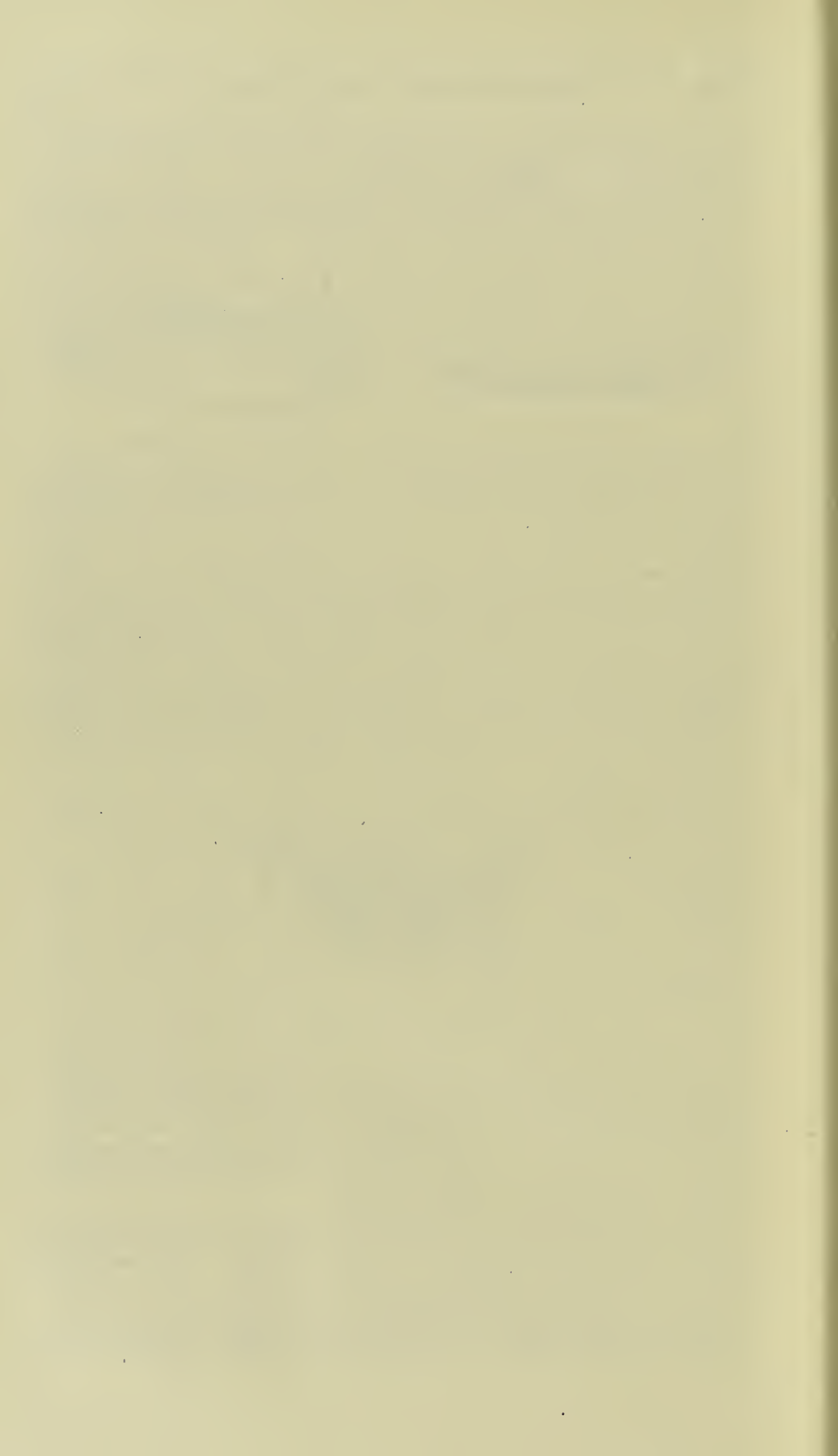
The premolar in advance of this, which is really the second according to the proper enumeration, has a single fang distinctly smaller than that of the canine. The two incisors, as determined by their alveoli, were also smaller than the canine, and had an erect position as in the monkeys, not procumbent as in the lemurs. In one specimen, the first is shown to be a little larger than the second, as in some monkeys. The mandibular rami were never coössified.

Description of the Type of Palæacodon vagus.

Of the upper teeth, the molars, figure 123, alone are known, if my determination that those of *P. vagus* refer to *Omomys Carteri* is correct. From what has just been said, I think there can be little doubt of this. The first molar is the largest of the series, and its more or less rectangular crown is made up of three principal cusps arranged in the form of a triangle, of which two are external and one is internal. The external cusps are imperfectly conical, slightly flattened on the outside, and connected with the internal by two distinct ridges (the trigonal ridges), upon which near the middle are developed two small, indistinct, intermediate cusps. The large internal cusp is imperfectly V-shaped, and around the inner side of its base there is a strong cingulum. Posterior and internal to this cusp, the cingulum develops a considerable swelling, which is the beginning of the posterior internal cusp of the higher monkeys. It is built out in such a way as to give a decidedly rectangular appearance to this part of the outline of the crown. This aspect is augmented by the unusual development of the cingulum at the antero-internal angle, where it likewise develops a small, though distinct cusp. In the second molar, which is slightly smaller than the first, the structure of the crown, as well as the arrangement of the cusps, is essentially the same. The postero-internal cusp is, however, not so well developed, and the internal outline of the crown is more rounded and less angular than that of the first molar. The last upper molar is reduced to about the same degree as that of the lower jaw. The intermediates of this tooth are very indistinct, and the internal cingulum is little developed. The inner part of the crown is narrower and more pointed.

The premolars are unknown, but in the type specimen the fangs of the fourth are to be seen. These consist of two external and one internal, as in the molars. Of the two external roots, the posterior seems to be the smaller.

The vertical range of this species is great, and specimens occur from the lowest to the highest levels of the beds.



[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XVII, FEBRUARY, 1904.]

Omomys pucillus Marsh.*Hemicodon pucillus* Marsh, this Journal, 1872, p. 22, Separata.

The type of this species, figure 124, consists of a fragment of a right mandibular ramus bearing the second molar, the structure of which agrees very closely with that of the corresponding tooth of *O. Carteri*, but the former is distinctly smaller. A second jaw fragment in which the second and third molars are preserved undoubtedly belongs to the same species. In my own collection, there are two jaw fragments in association with two superior molars, and in the Marsh collection there is one entire series of superior molars. These additional specimens, figures 125 and 126, furnish as complete a knowledge of the dentition as that described in the foregoing species. The dental formula of the lower jaw is the same as in *O. Carteri*, and with some few exceptions, which are of no more than specific importance, the details of structure are very similar. The chief distinctions separating *O.*

124



FIGURE 124. — Jaw fragment containing the lower molar of the right side of *Omomys pucillus* Marsh (type of *Hemicodon pucillus* Marsh); side and crown views; a little more than four times natural size.

125

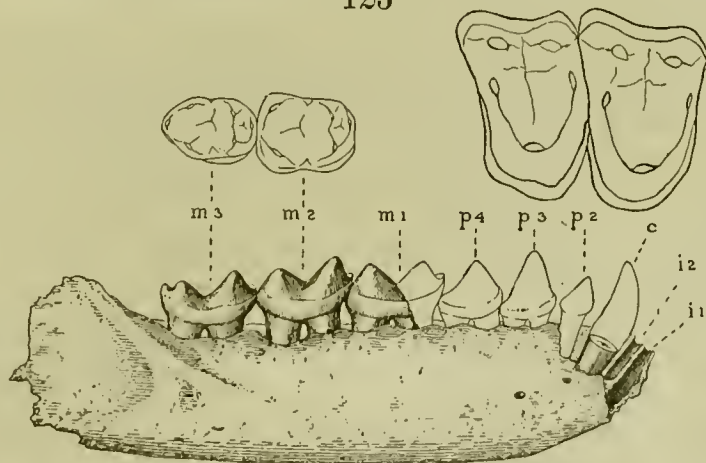


FIGURE 125. — Lower jaw and two superior molars of *Omomys pucillus* Marsh; side view of lower jaw, with side and crown views of teeth, and crown view of superior molars; the last are represented in outline five times natural size, while the lower jaw is a little less than three times natural size, and is drawn from three specimens.

pucillus from *O. Carteri* are the following: The species is considerably smaller; the last lower molar is slightly more reduced,

and there is a distinct ridge descending from the external cusp of the heel into the valley—a structure which is wanting in *O. Carteri*; the crown of the last upper molar is not so pointed internally; the postero-internal cusp is better developed upon the second than on the first molar; the intermediates are a little less distinct than in *O. Carteri*.

The species is thus far known from the lower and middle horizons of the Bridger.

Omomys Ameghini sp. nov.

A third still smaller species, which I refer provisionally to this genus, is represented by a fragment of a lower jaw of the left side, containing the second and third molars, figure 127. Besides being smaller in size than that of *O. pucillus*, the trigon is elevated above the heel to a much greater extent. This gives a somewhat insectivorous appearance to the teeth, but they are otherwise as in the species of *Omomys*.



FIGURE 126.—Crown view of three superior molars of the right side of *Omomys pucillus* Marsh; two and one-half times natural size.

FIGURE 127.—Jaw fragment of the left side of *Omomys Ameghini* Wortman; side and crown views; two and one-half times natural size. (Type.)

The last molar is little reduced, and the anterior cusp of the trigon is distinct in both the second and third.

The locality from which the specimen was obtained is not mentioned on the label, unfortunately, so that its exact horizon is unknown. The specimen was found by Mr. J. W. Chew.

Omomys uintensis Osborn.

Microsyops uintensis Osborn, Bull. Amer. Mus. Nat. Hist., 1895, p. 77; ibid., June 28, 1902, p. 202.

This species of *Omomys* was founded upon a fragment of jaw from the Uinta, containing the third and fourth premolars and the first and second molars. The specimen is preserved in the American Museum collection, and has recently been figured by Osborn in his paper on the American Eocene Primates. At the time of its description, Osborn referred the specimen to the genus *Microsyops*, but in his last paper that reference is considered erroneous. After a careful examination of the type and a detailed comparison with *Omomys*, I am fully convinced that it is the Uinta representative of this

genus, and is therefore the only Primate thus far known from the Uppermost Eocene of North America.

Its relationship is at once seen in the elevated character of the crown of the third premolar, as well as in the general agreement in the structure of the teeth. It is, however, the largest species of the genus known, and exhibits a marked advance in the structure of the teeth, in the more widely separated and distinct condition of the internal cusp of the fourth premolar, as well as in the absence of the anterior cusp of the trigon on the second molar. The Bridger species are all smaller and more primitive.

Hemiacodon gracilis Marsh.

Hemiacodon gracilis Marsh, this Journal, September, 1872, Separata, August 13, 1872, p. 21; *Omomys gracilis* Osborn, American Eocene Primates, Bull. Amer. Mus. Nat. Hist., June, 1902, p. 173.

This is one of the most abundant species of monkey in the Bridger formation, and as far as the specimens show is confined to the upper levels of the horizon. The type upon

128

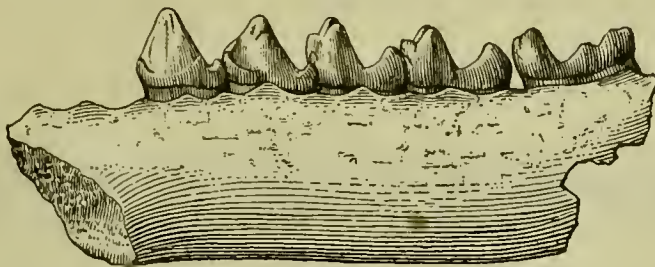


FIGURE 128.—Portion of right mandibular ramus of *Hemiacodon gracilis* Marsh; inside view; two and one-half times natural size. (Type of the genus and species.)

The elevation of the summit of the crown of the third premolar is greater in the type than in other specimens, on account of being partially out of the socket.

which Professor Marsh established the genus and species consists of a considerable part of a right mandibular ramus, figure 128, bearing the third and fourth premolars and the three molars in excellent preservation. The specimen also exhibits the alveoli for the second premolar, canine, and the two incisors, but is not sufficiently complete in front to admit of a determination of the number of incisors beyond all question. As compared with *Omomys Carteri*, the teeth of the lower jaw display in their structure a striking similarity to those of this species, and it is not at all surprising that Professor Marsh should have referred the two to the same genus. The chief differences consist in the enlargement of the first incisor and the reduced condition of the second incisor, canine, and second premolar, as well as in the better development of the internal cusp of the fourth premolar in *Hemiacodon gracilis*. The relations of the teeth in the front part of the jaw, I regard as

of more than specific importance, and these constitute in my estimation the main characters upon which the generic distinction rests.

In the molars the anterior cusp of the trigon is distinct in all, but least so in the last. There is likewise a very faint indication of a posterior median cusp in the heel of the first and second molars in the type, but in other specimens it is apparently absent. The posterior portion of the crown does not widen so rapidly as is the case in *Omomys Carteri*, the

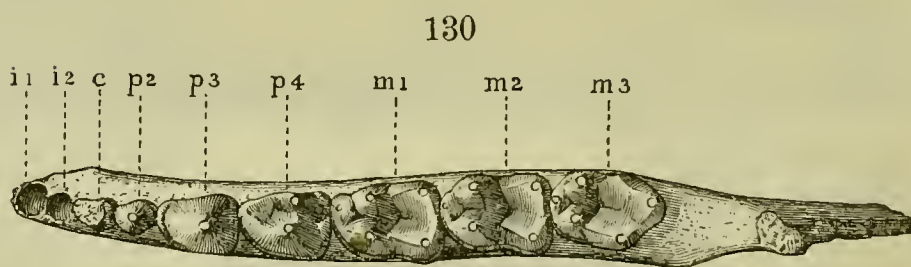
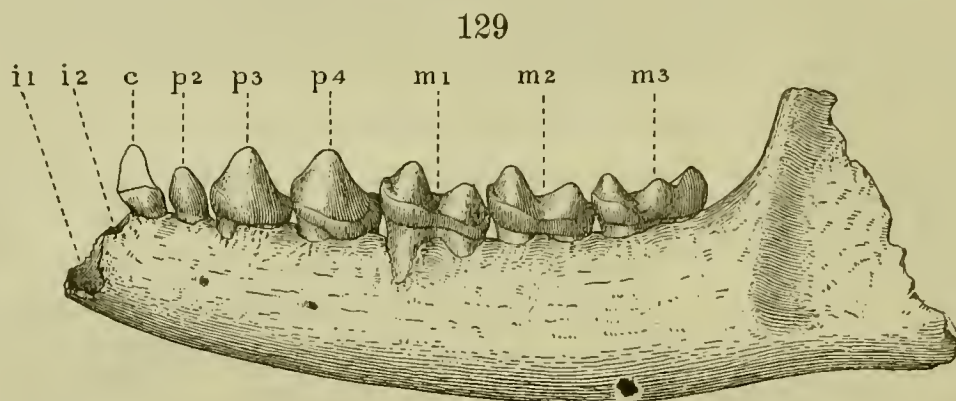


FIGURE 129.—Left lower jaw of *Hemicodon gracilis* Marsh; external view; two and one-half times natural size; drawn from two specimens.

FIGURE 130.—Crown view of the same specimen.

In the drawing the alveolus of the first incisor does not appear as large as it actually is. The upper portion of the alveolus is broken away, so that only the bottom of the cavity is shown.

transverse diameter of the anterior and posterior moieties being more nearly equal. The fourth premolar is more advanced in structure than the corresponding tooth of *O. Carteri*. The third premolar in the type shows no trace of an internal cusp, but in some other specimens in the collection, of which forty or fifty individuals are represented, there is a distinct rudiment of this structure to be seen.

The second premolar and canine, figures 129 and 130, are preserved in several specimens, and their reduced size, as compared with the third premolar and the corresponding teeth of *O. Carteri*, is very evident. The incisors are not preserved in any specimen in the collection, but in several the front part of the jaw is sufficiently complete and well preserved to permit the alveoli to be made out with certainty. From these the number is shown to be two, of which the first is considerably larger than the second. The teeth were implanted in an uninterrupted

series and there is good evidence that the incisors were not very procumbent in position. The two halves of the lower jaw were not coössified, even in the most aged individuals.

In the upper jaw, figure 131, the teeth occur, in many examples, in association with those of the lower series. The structure of the molars is distinctive, not only by reason of the rather sharply quadrate outline of their crowns, but also because of their relatively great transverse extension. The first and second are subequal in size, and the third is considerably

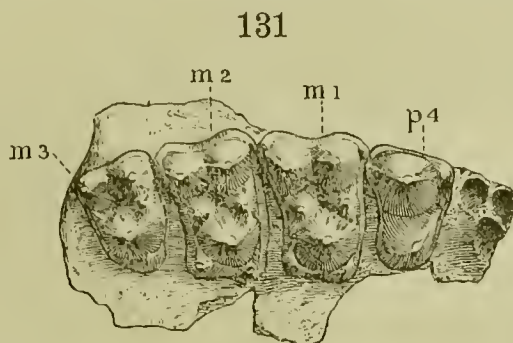


FIGURE 131.—Superior molars and fourth premolar of *Hemicodon gracilis* Marsh; crown view; two and one-half times natural size.

The representation of the forward extension of the internal cingulum of the molars, as well as the size of the internal cingular cusp, is somewhat exaggerated.

reduced. The external cusps are moderately flattened upon their outer side, especially the posterior one, and they are bordered externally by a strong basal cingulum. The intermediates are unusually well developed, and there is a large internal pyramidal cusp. A small postero-internal cusp is developed from the cingulum, which continues forward around the inner side of the crown, and gives rise to a moderately strong subsidiary internal cusp. The extent to which this cusp, as well as the forward extension of the cingulum, is developed, however, appears to vary in the different specimens; in some the cusp is very distinct, while in others it is scarcely visible. The fourth premolar has single external and internal cusps. The third and fourth premolars are implanted by three roots, two external and one internal. The teeth anterior to these are unknown with certainty. The enamel is finely rugose in both the upper and the lower teeth.

In the fragment of a maxillary here figured, the anterior limits of the malar can be easily made out. It is thus shown that it does not reach forward to the lachrymal, but leaves the maxillary a considerable share in the anterior boundary of the orbit, as in the monkeys. The rather small, single, infraorbital foramen is situated above and opposite the posterior edge of the third premolar, about in the same relative position as that of the squirrel monkey. The maxillary gives further evidence of proportionally large orbits, and if the superior dental formula was the same as that for the lower jaw, the muzzle must have been considerably abbreviated. The whole aspect is, in

fact, not only characteristically Primate, but one considerably advanced.

In one specimen the head of a humerus is associated with a fragment of a lower jaw, which is apparently the proper size for *Hemiacodon gracilis*. The character of this bone is distinctly Primate. Among the living forms, it bears a closer resemblance to the humerus of *Propithecus* and *Avahis* than to any other with which I have compared it. This is particularly evident in the relatively great development of the lesser tuberosity and its inward and backward projection from the articular head. In this respect it also resembles the humerus of *Tarsius*, *Hapale*, and *Cebus*, although not so closely as it does that of the genera above mentioned. The large size of the lesser tuberosity is likewise a conspicuous feature of the humerus of *Limnotherium*, from which it may be concluded that it is a primitive character.

Professor Marsh has given the following measurements of the type :

Longitudinal extent of the nine lower teeth	20.5 mm
Extent of premolar and molar series	17.2
Extent of true molars	11.0
Antero-posterior diameter of last lower molar	4.0
Transverse diameter of last lower molar	2.4
Depth of jaw below last lower molar	6.3

The type specimen was found near Henry's Fork, by Mr. G. G. Lobdell, Jr. The other specimens of the collection are from the same horizon.

Hemiacodon pygmæus sp. nov.

A second species of this genus is indicated by a single superior molar, figure 132. Under ordinary circumstances, I

132



FIGURE 132.—Superior molar of *Hemiacodon pygmæus* Wortman; crown view; four and one-third times natural size. (Type.)

should deprecate the proposal of a new specific name upon such an incomplete specimen, but in the present instance the relationship is so clearly indicated and the differences are so patent, that I do not hesitate to follow this otherwise reprehensible practice.

The tooth in question displays its undoubted affinities with the molars of *Hemiacodon gracilis*, in its quadrate outline, its relatively great transverse extension, and the general arrangement of the cusps. The external cusps are somewhat more conical than those of *H. gracilis*, but the intermediate and internal cusps are practically the same as in that species. The great difference is seen in the size, *H. pygmæus* being but little more than one-half as large as *H.*

gracilis. It is possible that the tooth pertains to the small species described as *Omomys Ameghini*, but I do not think it likely.

The locality is not clearly indicated on the label, but the specimen was associated with other fragments from Dry Creek, which gives it an upper middle position in the Bridger horizon.

Euryacodon lepidus Marsh.

Euryacodon lepidus Marsh, this Journal, August and September, 1872, p. 33, Separata.

Professor Marsh in describing this genus and species says: "A small mammal, doubtless an insectivore, is represented by a fragment of an upper jaw containing the last two molars in perfect condition. Our collections contain other characteristic fossils which appear to be specifically identical with this specimen. The teeth preserved agree nearly in the composition of their crowns with the molars described by Dr. Leidy under the name *Palæacodon verus*, but each has its inner margin produced into a small tubercle. In the penultimate upper molar, this tubercle is especially prominent. The outer margin, also, of these molars has but a single faint indentation between the external cusps. Both teeth are surrounded by a distinct basal ridge. The specimens preserved indicate an animal about as large as a weasel."

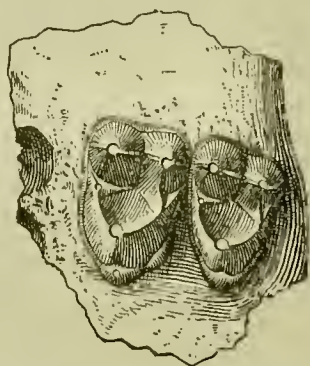
Besides the type, there are in the collection four other examples which I refer to this species. One of these is a fragment of an upper jaw bearing the second and third molars, just as in the type; and three lower jaw fragments, which, however, in no instance are associated with the upper molars. The reference of the latter to this species, therefore, contains an element of uncertainty.

The upper molars, figure 133, resemble those of *Omomys Carteri*. In the second molar of this latter species, however, figure 123, the anterior internal cingular cusp is not developed, while in *Euryacodon lepidus* it is strong. The last molar, moreover, in the latter species is a little less reduced and the crown is not so narrow and pointed, especially on its internal or lingual side. The external cusps are rather conical, and the intermediates are moderately well developed. The homologue of the main postero-internal cusp has a somewhat more external position, and this portion of the crown has a distinctly less rectangular outline than the corresponding tooth in *Omomys Carteri*.

In the lower jaw, figure 134 (if the specimens are correctly referred to this species), the molars only are known. The structure of their crowns is quite different from that of any species of *Omomys*. The anterior cusp of the trigon is well

developed in the first molar, and has nearly the same relations as in the corresponding tooth of *Omomys Carteri*. In the second molar, however, this cusp has a much more posterior position and is decidedly smaller, while in the third it is completely absent. The last molar is narrower and more reduced than in *Omomys*, and the heel lacks the distinct pointed cusps seen in all the species of that genus. The crowns of the upper molars, especially that of the second, are almost as wide in front as behind, being in marked contrast with the molar

133



134

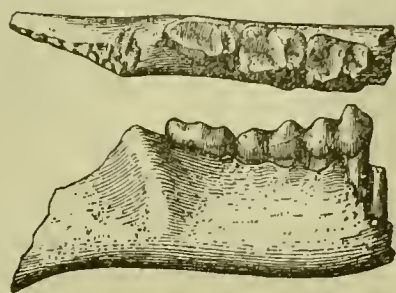


FIGURE 133.—Two superior molars of *Euryacodon lepidus* Marsh; crown view; a little less than four times natural size. (Type of genus and species.)

FIGURE 134.—Lower jaw fragment of *Euryacodon lepidus* Marsh; side and crown views; two and one-half times natural size.

crowns of the species of *Omomys*. Thus it will be seen that the lower molars of *Euryacodon* are more advanced than those of *Omomys*, and there can be apparently very little doubt that they represent distinct genera.

The complete dentition of the lower jaw is unknown, and I have provisionally referred the genus to the Omomyinæ. A comparison with the type of Cope's *Anaptomorphus æmulus*, from the lower horizon of the Bridger beds, shows many points of similarity. As is well known, the type of this latter species consists of a lower jaw in which the first and second molars are present, but the third is missing from the specimen. In *Anaptomorphus* the anterior cusp of the trigon has disappeared in both the first and second molars, which at once establishes the fact that it is at least a different species from *Euryacodon lepidus* and the most advanced form of Primate thus far known from the American Eocene. It is upon this account that I have chosen to regard *Euryacodon* and *Anaptomorphus* as distinct from each other, until the full dentition of the former and the upper teeth of the latter are more fully known. If *Euryacodon* is eventually found to possess only two premolars in the lower jaw, it will then probably be necessary to unite the two genera under the name *Euryacodon*, since the latter has distinct priority over *Anaptomorphus*.

[FROM THE AMERICAN JOURNAL OF SCIENCE, VOL. XVII, MARCH, 1904.]

On the Affinities of the Omomyinæ.

As I have already fully stated, my arrangement of this group of Primates under the Paleopithecine division of the Anthropoidea is only provisional. The incompleteness and frag-

135



136

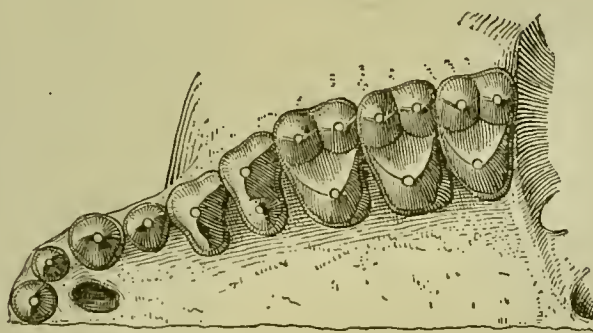


FIGURE 135.—Lower jaw of *Tarsius spectrum*; crown view; two and one-half times natural size.

FIGURE 136.—Upper teeth of *Tarsius spectrum*; crown view; two and one-half times natural size.

mentary condition of the remains of all the species thus far known precludes the possibility of determining their affinities and position with any great degree of exactness. It has been pointed out that the dentition of the lower jaw, and presumably that of the upper jaw also, in all the species in which it is definitely known, is represented by two incisors, a canine, three premolars, and three molars. This number differs from that of *Tarsius*, figure 135, in the presence of an additional incisor, there being only a single pair in the lower jaw of that genus. The structure of the lower molars and premolars accords well, moreover, with that of *Tarsius*, which undoubtedly represents a very generalized pattern among the Primates, and one from which it is possible to derive all the more complex types of the higher forms. In the structure of the superior molars, all the species of the Omomyinæ have apparently advanced beyond

the *Tarsius* stage, figure 136. This is seen in the continuation of the cingulum forward, around the internal face of the crown, and the development of a distinct cingular cusplule internal to the main antero-internal cusp. In the two external roots of the fourth superior premolars, however, the species of the *Omomyinæ*, as far as known, agree with *Tarsius*. This is very probably a generalized character, also, since there is very strong presumptive evidence that the single external root of the third and fourth premolars, common in the higher apes, is the result of degeneration caused by the shortening of the face.*

137



138



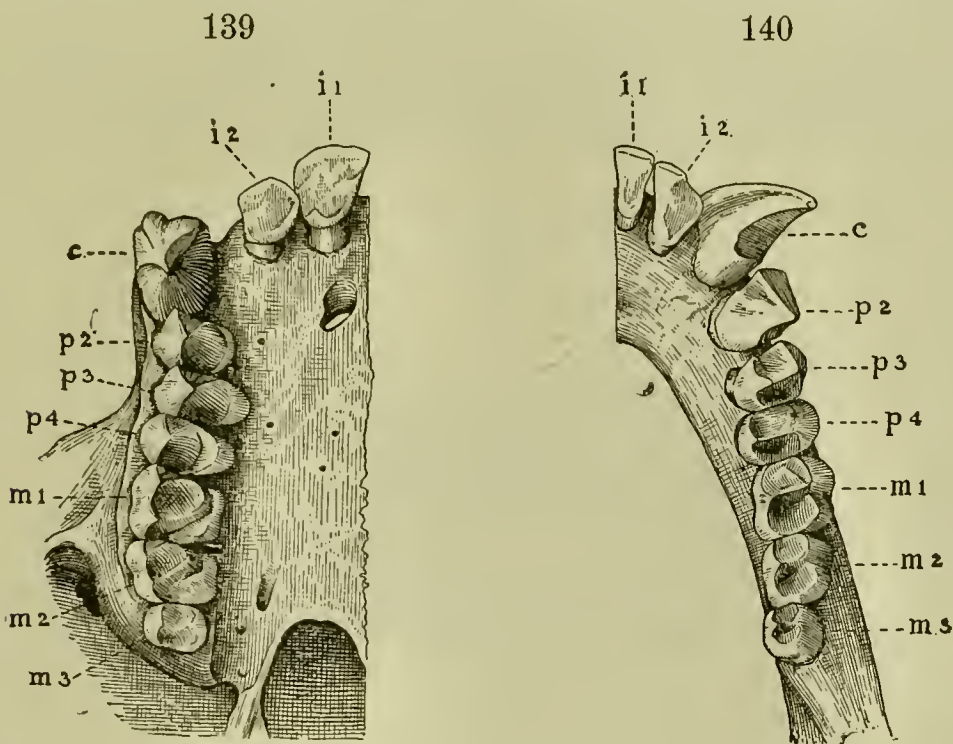
FIGURES 137, 138.—Upper and lower teeth of *Cebus apella*; crown view; three halves natural size.

The final determination of the exact relations of these forms to *Tarsius* must await the discovery of the lachrymal region, as well as of the structure of the limbs and feet.

It is proper, however, to call attention in this connection to some striking resemblances which this group exhibits to certain of the South American apes, notably the capuchins and squirrel monkeys. In the former of these, of which *Cebus apella*, figures 137 and 138, is a good example, the upper molars present a characteristic and in many respects a peculiar and distinctive pattern. The first molar is the largest of the series

* In *Cebus* the external root of the third and fourth premolars is either deeply grooved or completely divided at the end. This is likewise true of *Mycetes*, as well as of many species of Old World apes. An example of the fusion of the external roots is seen in the last molar of many species of apes where it is strongly reduced, as in *Cebus*, *Chrysotrux*, and others.

and the last is the smallest, being considerably reduced. In the crowns of the first and second, the trigonal ridges are distinct, and there is a prominent intermediate cusp present. The postero-internal cusp is well developed and has a position much more internal to the antero-internal than is generally the case in molars of the higher Primates. Because of its position this cusp is more widely separated than usual from, and does not develop a close connection with, the original trigon. There is a strong cingulum continued forward around the inner face of the crown, from which a small cingular cuspule is formed internal to the main antero-internal cusp. This is most dis-



FIGURES 139, 140.—Upper and lower teeth of *Chrysothrix sciurea*; crown views; twice natural size.

tinct in the second molar, although a considerable rudiment of it is seen in the first. In the squirrel monkey, *Chrysothrix sciurea*, figures 139, 140, and 141, the superior molars exhibit practically the same structure as those of *Cebus*, the only important difference between the two being that the posterior intermediate cusp is not distinct in *Chrysothrix*. The cingulum is continued around the inner face of the crown in both the first and second molars in the same way as it is in *Cebus*; but its development is greater in the first molar than in the second, whereas in *Cebus* the cingulum and the anterior cingular cusp are stronger in the second than in the first.

This peculiarity in the structure of the molars is not found in any other South American ape, nor, as far as I am aware, in any other living species of Primate in any part of the world. It is highly significant, therefore, that so unusual a modification and one so entirely unique among the Primates should be

met with in its incipient stages in the typical North American Eocene group *Omomyinæ*. As we have just seen, this character is found in the upper molars of all the species, and may be said to be especially characteristic of them. We know, moreover, that they are Primates; that the dental formula for the lower jaw and presumably for the upper is the same as in the *Cebidæ*; that the number, structure, and relations of all the teeth of certain species, at least, so completely fulfil the requirements and conditions which one would naturally seek in an ancestor of these living *Cebidæ*, as to make it scarcely possible to believe that such striking resemblances can be altogether accidental. In fact, this is the only group of Primates that has ever been found, among either living or extinct forms outside of South America, which exhibits any approximation to any of the *Cebidæ*, and until some tangible evidence to the

141

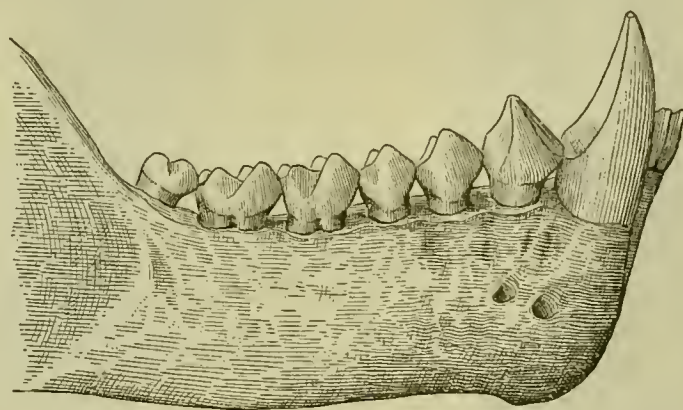


FIGURE 141.—Lower jaw of *Chrysothrix sciurea*; side view; twice natural size.

contrary is forthcoming we are compelled to regard these extinct North American types as the source from which the ape fauna of the Neotropical realm had its origin.

It has been assumed by some who have sought to solve the problem of the origin of the *Cebidæ*, that they were derived from Africa, and making their way thence across an Antarctic land connection, thus reached South America. This view is based upon the presence in the Patagonian Miocene of the remains of numerous Marsupials closely allied to those now living in Australia, which argues strongly for a land connection with that continent during the Tertiary. From resemblances among certain living species from South America to those of Africa, as well as among some of the extinct forms, it is further assumed that this land bridge extended to Africa, and that there was an interchange of species between the two Hemispheres. While this may perhaps satisfactorily account for the presence of those African types in South America, it does not

apply to its simian population. The insuperable objection to an African origin for the Cebidæ is found in the complete absence of any group of Primates, either fossil or recent, in the tropics or any part of the Eastern Hemisphere, which exhibits any near affinities with the New World apes. Africa is to-day the congenial home of a large and varied lemuroid and simian population in which species of the highest and lowest degree exist side by side. Something is known, moreover, of the ancient representatives of this Primate fauna from the Tertiaries of Europe and Asia, but whether we consider the living or extinct forms, not a single species has yet been brought to light among them which does not proclaim its distinctive relationship and bear the unmistakable stamp of its affinities with the Primates of the Old World. Among the monkeys and apes, this is so positive that no one has ever ventured to assert the contrary.

In like manner, the fossil monkeys of South America exhibit the closest relations to those species now living there. Ameghino has found the remains of apes in the Santa Cruz Miocene of Patagonia, which are closely allied to, and hardly distinguishable from, the living *Cebus* of the Amazonian tropics. They exhibit no traces of relationship with any species inhabiting Africa. Any direct connection between the Cercopithecidæ and the Cebidæ may be dismissed, therefore, as utterly untenable and unsupported by a single fragment or vestige of evidence. Neither can it be logically argued that the Cebidæ, originating in Africa, migrated thence in a body to the New World. No assignable reason can be given why all the genera, species, and individuals of so large and varied an assemblage as the New World apes must have been, even prior to the Miocene, should have suddenly quitted the home of their birth, without leaving behind a single representative or trace which would furnish a clue to their former presence in a region now so well fitted, apparently, for ape existence. Any such vestige, however, is singularly absent, and from whatever point of view we choose to regard it, such a hypothesis appears simply impossible.

In connection with the evidence which I have already brought forward in favor of the North American origin of the Edentata,* a similar origin for the South American Primates, which is the only alternative hypothesis conceivable, is placed upon an extremely probable, if not absolutely secure, foundation, and is entitled to infinitely greater consideration than any purely conjectural origin of these forms, wholly without evidence in its support. I have formerly suggested that the so-called Litopterna were direct derivatives of *Meniscotherium* of our Wasatch

* The Ganodonta and their Relationship to the Edentata, Bull. Amer. Mus. Nat. Hist., vol. ix, pp. 59-110, 1897.

beds, and I now further venture to believe that all the South American Ungulates, including the Toxodonts, Typotheres, Astrapotheres, etc., are but modified descendants of our North American Condylarths, and were derived from the same region as the Edentates and Primates.

Subfamily Anaptomorphinæ.

As already indicated, the genera of this subfamily agree in having only eight teeth in the lower jaw. It is in all probability not a natural assemblage, since it is tolerably clear that the missing teeth are not the same in the various genera. Until this is more fully determined by better specimens, the present classification must be regarded as by no means final. The genera composing this group can be distinguished by the following characters:

Lower molars having four cusps on trigon, all distinct; heel of last molar with four cusps; first and second molars not especially wider behind than in front; last molar largest of the series; fourth lower premolar with moderately strong internal cusp and rudimental heel; third premolar with very small rudiment of internal cusp; canine larger than second premolar or incisor; only one pair of incisors in lower jaw (?); superior molars tri-tubercular, with more or less rectangular outline; intermediate cusps small, but distinct; postero-internal cusp well developed on crown of first and second molars, but not distinct on third.

Washakius.

Lower molars having only two cusps on trigon; last molar unknown in type; first and second molars widening rapidly behind; third and fourth lower premolars without internal cusps; canine larger than incisors; second premolar absent in type; two pairs of incisors in lower jaw; upper teeth unknown in type.

Anaptomorphus.

Lower molars having only two cusps on trigon, a vestigial anterior cusp on first; heel of last molar with three cusps; first and second molars wider behind than in front; last molar not reduced; fourth lower premolar with well-developed internal cusp; second tooth of the series vestigial and implanted external to the tooth line; superior molars quadritubercular.

Necrolemur.

Washakius insignis Leidy.

Washakius insignis Leidy, Contr. Ext. Fauna West. Terr., 1873, p. 123.

Leidy's type of this genus and species consists of a fragment of a lower jaw carrying the second and third molars so much worn as not to display the arrangement of the cusps. Up to the present, this specimen has remained the sole example of the species, which on account of its imperfect representation

has had no very definite standing. Its relationship to the Primates, even, has been called in question, and it has been thought by some to belong to the Rodentia. There are, however, about ten individuals represented in the Marsh collection, which I do not hesitate to refer to Leidy's genus and species. The most conclusive point in this identification is found in the extra cusp on the inner posterior surface of the trigon of the lower molars, the remains of which can be still plainly seen in the much-worn molars of Leidy's type. In one specimen in the Marsh collection, there is in association with the lower teeth a fragment of an upper jaw containing two molars, so that the structure of the teeth can be made out with a reasonable degree of accuracy.

The complete dental formula of the lower jaw is not known with absolute certainty, but in one specimen the front of the jaw is sufficiently preserved to render it highly probable that there was but a single pair of incisors. At all events, if the

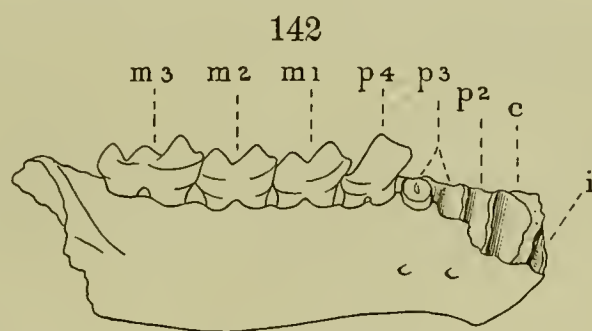


FIGURE 142.—Right lower jaw of *Washakius insignis* Leidy; side view; two and one-half times natural size; drawn from two specimens.

middle incisors were present they must have been exceedingly small. A good idea of the relations of the lower teeth can be had from the accompanying illustration, figure 142, which was drawn from two specimens. The outer side of the front of the jaw is injured so that the lower part only of the alveolus for the incisor is shown; this is seen to be smaller than that for the canine. Following this without diastema is a small alveolus for the second premolar, after which come the double-rooted third and fourth premolars. The crown of the second, figure 143, has a simple pointed summit, to which is added a small anterior basal, and a stronger internal cusp. That of the second has a similar structure but the internal cusp is better developed. In both the third and fourth premolars, the internal cusp is placed rather low upon the crown. The heel is rudimental.

The molars are peculiar in the composition of their crowns, by reason of the possession of an extra cusp situated internal and a little posterior to the main antero-internal cusp. The trigon thus has four cusps, a condition unknown in any other species of Primate. The remaining cusps of the trigon are

normal in their relations to the crown, the anterior one being distinct in all the molars. The heel of the first and second molars has the usual two cusps and is but little wider than the anterior portion or trigon. In the last molar, however, the heel has four cusps, which is again a unique character among

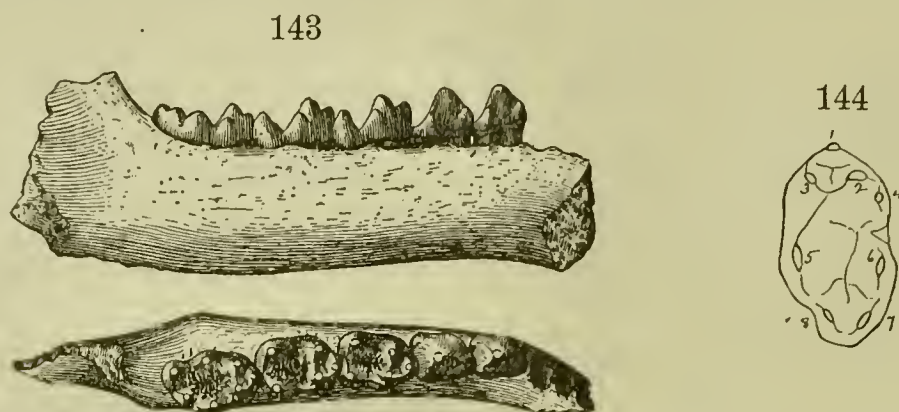


FIGURE 143.—Left lower jaw of *Washakius insignis* Leidy; inside and crown views; two and one-half times natural size; drawn from two specimens.

FIGURE 144.—Last left lower molar of *Washakius insignis* Leidy; crown view; five times natural size.

the Primates. An outline view of the grinding surface of the crown of the last lower molar of the left side, enlarged five times, is given in figure 144, which represents accurately the arrangement of the cusps. The enamel of the crowns of all



FIGURE 145.—Last two superior molars of the right side of *Washakius insignis* Leidy; crown view; four times natural size.

The postero-internal cusp of the second molar is not represented strong enough in the drawing.

FIGURE 146.—Left superior maxillary of *Washakius insignis* Leidy; crown view; two and one-half times natural size.

the lower teeth is strongly wrinkled, that occupying the valley of the heel especially so.

The fragment of upper jaw associated with the lower teeth, figure 145, contains the second and third molars. The second molar is larger than the third, although the disparity in size is not so great as in *Omomys* or *Hemiacodon*. The crowns are

tritubercular, with only a moderate development of the postero-internal cusp, and the cingulum is not continued forward around the internal face of the crown and does not develop the internal cingular cuspsule seen in *Omomys* and *Hemiacodon*. The outer cusps are slightly flattened externally, and the intermediates are moderately developed. The enamel is much wrinkled, particularly that upon the inner portion of the crown. A second specimen, representing upper teeth, consists of a large part of the superior maxilla containing all the molars and the third and fourth premolars, figure 146. It also exhibits the alveoli of the second premolar, canine, and probably two incisors; that of the first incisor is, however, very indistinct, and one can not be sure that it was actually present.* In this specimen the second molar is larger than either the first or third, which are subequal. The postero-internal cusp is more distinct in the first molar than in the second or third. The premolars display single external and internal cusps, with a strong postero-internal cingulum tending to the formation of an additional cusp. The canine, as indicated by the size of the alveolus, is larger than the outer incisor or second premolar, and, as in the lower jaw, the teeth were implanted in a continuous row. The infraorbital foramen is single and issues above the anterior border of the third premolar in the same relative position as in *Hemiacodon*. The malar did not reach the lachrymal, thus leaving the maxillary a large share in the anterior boundary of the orbit, which was enlarged.

From these many resemblances to the Primates, there can not apparently be any question of the affinities of the genus, notwithstanding the peculiarities of the structure of the lower molars. It seems to have left no modified descendants, however, in the existing fauna.

Anaptomorphus æmulus Cope.

Anaptomorphus æmulus Cope, Proc. Amer. Philos. Soc., October, 1872 p. 554.

This genus and species were proposed by Cope upon the greater portion of a left mandibular ramus now preserved in the American Museum collection, which, as far as I am aware, is the only specimen of this species known. The jaw carries the first and second molars and the fourth premolar, together with the alveoli for all the remaining teeth, eight in all. The formula has been generally considered to be two incisors, a

* That which leads me to suspect the presence of two incisors in the upper series is the sharp inward curvature of the lower jaw near the symphysis, giving a greater transverse width in this region of the mouth. There would thus be a considerable gap left between the outer incisors and the median line. I think there can be little doubt that this space was occupied by a central pair of incisors.

canine, two premolars, and three molars, principally for the reason that the alveolus for the third tooth is enlarged after the manner of a canine, while the two in advance of it are small and hence have been thought to represent incisors. This determination is very probably correct, but it can not be accepted as final until the upper teeth are fully known. The extreme reduction in the number of premolars is a condition more advanced than that found in any other species of Primate, either living or extinct, in the Western Hemisphere; and that it should have taken place as early as the Eocene is indeed remarkable. In agreement with this reduction, it may be noted, however, that the structure of the lower molars is further advanced than that of any of its contemporaries in the Bridger. This is seen in the loss of the anterior cusp of the trigon from all the molars, and their consequent reduction to the four-cusped stage. I have already called attention to certain resemblances in the structure of the molars between *Anaptomorphus* and *Euryacodon*, but the former exhibits a greater advance in the modification of these teeth.

A second species, *A. homunculus*, was described by Cope from the now famous cranium found by me in the Basin of the Big Horn, in 1881. This cranium, together with a second specimen (No. 41 of the American Museum collection) which I also discovered in 1891, in the same region, has recently been refigured by Osborn.* These drawings are beautifully executed, but it is to be regretted that the skull is represented as complete in front, which is by no means the case. Osborn's figure gives the impression that the face is as much shortened and as reduced as in the highest type of living ape. Cope's original figure, in his *Tertiary Vertebrata*, is far more accurate in that it represents the entire anterior portion of the skull as missing. After a most careful study of the remains of this species in the American Museum collection, I find myself unable to agree with Cope in regard to the dentition of the cranium in question, or with Osborn concerning the dentition of the additional specimens. Cope determined the premolar dentition of the upper jaw to be two, and Osborn gives the number of lower premolars as three. The facts may be briefly stated as follows: In the cranium, there is evidence of the presence of seven teeth; of these, three are undoubtedly molars, and the remainder incisors, canine, and premolars; the most anterior tooth indicated is represented by an alveolus; the next is a pointed single-rooted tooth separated by a short diastema from those behind; the two following teeth are undoubtedly premolars, with single external and internal cusps.

* American Eocene Primates, Bull. Amer. Mus. Nat. Hist., 1902, p. 200.

The element of uncertainty comes in the determination of the nature of the first two teeth, and I can find no proof that the single pointed tooth is the canine, as held by Cope and Osborn. There is certainly no indication of the maxillo-premaxillary suture to be found, and the tooth in question may quite as well be a premolar as a canine. In fact, in the fragmentary maxilla of the other specimen (No. 41) there is evidence of a tooth with more than a single root in advance of the two premolars, and if the two specimens belong to the same species, which is more than likely, there were certainly three premolars in the upper jaw. In like manner I am unable to discover any conclusive evidence in favor of Osborn's statement that there are three premolars in the lower jaw, together with a canine and two incisors. I am strongly inclined to believe that there were three premolars in the lower jaw, however, and that Osborn's determination is correct; but at the same time the specimens are not sufficiently perfect to furnish conclusive proof of the fact. Nor can it be demonstrated at the present time that the Big Horn and the Bridger species belong to the same genus. Upon general considerations, I think it most unlikely. I believe, moreover, that the Big Horn species is a type with three premolars above and below, and that it is generically distinct from the Bridger *Anaptomorphus*. I have refrained from proposing a new genus for this species, preferring to let the matter rest until the dentition of both the Big Horn and the Bridger forms is more fully known.

In the matter of the restoration of the skull, I can find no warrant for the extremely abbreviated face which Osborn gives in his drawing. The contour of the muzzle was undoubtedly much more like that of *Tarsius*, with which the cranial anatomy so closely agrees. Apparently very little consideration has been given to these resemblances between *Tarsius* and the Big Horn fossil, which Cope pointed out. It will perhaps be well to recall them here, with some emendations and additions. They are as follows: (1) The species are of about the same size, both being small; (2) the brain development is relatively large; (3) the brain projects well backward beyond the foramen magnum, so as to overhang the occiput; (4) there is no sagittal crest; (5) the face is considerably shortened, and the orbits are large; (6) the canal for the internal carotid pierces the petro-tympanic; (7) the dentition is very probably the same, with the exception of the loss of one pair of incisors in the lower jaw in *Tarsius*; (8) the structure of the molars and premolars is very similar; (9) the bullæ are much inflated, and the external wings of the pterygoids extend backward, so as partially to enclose the bullæ externally; (10) the lachrymal extends out upon the face, and the opening of the lachrymal

canal is external to the orbit; (11) although not positively known, the relations of the lachrymal and malar are the same.

There are some differences to be noted, but they relate entirely to the assumption of modernized features on the part of *Tarsius*. Upon the whole, the resemblances are so striking and strongly marked that apparently there can not be the slightest question, not only of the close relationship between the two forms, but of the further important fact of their common origin. I have already suggested that the place of this origin was within an ancient circumpolar land.



FIGURE 147.—Right lower jaw of *Necrolemur Edwardsi* Filhol; enlarged several times. (After Filhol.)

FIGURE 148.—Three lower molars of *Necrolemur Edwardsi* Filhol; crown view; enlarged. (After Filhol.)

Necrolemur may or may not belong in this series. If it does, it is by no means as closely allied to *Tarsius* as the American species. It has been suggested by Leche that it is related to the Indrisine lemurs, and there is indeed much in favor of such a view. If one compares the lower jaw of *Necrolemur Edwardsi*, figure 147, with that of *Propithecus diadema*, the resemblance in general form is at once apparent. The loss of the vestigial second tooth in *Necrolemur* would give the formula of the Indrisinæ, which is seven teeth in the lower jaw. *Necrolemur* differs from *Tarsius*, moreover, in the more advanced condition of the molars. In the lower jaw the anterior cusp of the trigon, figure 148, has completely disappeared, and in the upper jaw the molars are almost fully quadritubercular. *Microchærus* in all probability comes in the same group, and when more fully known should furnish a closer approximation to the Indrisinæ than *Necrolemur*, on account of the development of a mesostyle in the upper molars. A further character in which *Necrolemur* resembles the Indrisinæ is the lack of differentiation of the anterior teeth into incisors and canines, as well as their tendency to the procumbent position.

